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ERRATA

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On page 363 of the October 1933 issue (Volume XIV, No. 4) a printer's error occurred in the paper by Gray and Treloar "On the Enumeration of Insect Populations by the Method of Net Collection." The radical should have been continued over the entire quantity for σ_x.

As printed:

$$\sigma_x = \sqrt{\frac{\sum(x - \bar{x})^2}{N}} = \sqrt{\frac{\sum x^2}{N}} - (\bar{x})^2,$$

Should read:

$$\sigma_x = \sqrt{\frac{\sum(x - \bar{x})^2}{N}} = \sqrt{\frac{\sum x^2}{N} - (\bar{x})^2}.$$

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On page 237 of the July 1934 issue (Volume XV, No. 3) in the third line from the bottom of the second paragraph, 'figure 10' should read 'figure 9.'

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THE VEGETATION OF CAT ISLAND, MISSISSIPPI [1]

WM. T. PENFOUND AND M. E. O'NEILL

Tulane University of Louisiana, New Orleans

Ecologists have eagerly seized the opportunity of studying plant succession on relatively barren areas where the changes are rapid and plainly evident. Such an opportunity is provided at Cat Island, a continental island some nine miles south of Gulfport, Mississippi. The island presents bare areas of fresh and brackish water, a changing sand dune topography, and many denuded forest and marsh areas. A visit to the island in March, 1931, indicated the desirability of vegetational study, and four subsequent trips were made with Mr. Horatio Weston of Logtown, Mississippi, to whom the authors are greatly indebted.

LOCATION AND CLIMATE

Cat Island is one of a chain of continental islands separating Mississippi Sound from the Gulf of Mexico. This chain includes Cat, Ship, Horn, Petit Bois, and Dauphine Islands, and extends from southwestern Mississippi to Mobile Bay, Alabama (fig. 1). These islands are situated at an average distance of twelve miles from the mainland and were undoubtedly connected with it in the distant past. This contention is supported by the fact that Mississippi Sound is very shallow (7–14 ft.), with a bottom composed mainly of hard clay which seems to be identical with the clays of the late Biloxi formation (Lowe, '19). The islands are mainly of fine to medium white sand built upon a base of black, peaty mud, sandy in the easterly islands but containing more clay toward the west. The source of the clay or muck is the fine sediment brought down by the Mississippi and Pearl Rivers and distributed by offshore currents.

Cat Island is the most westerly of the islands and is less than four miles from Isle au Pitre, a muck island, the last outpost of a former delta of the Mississippi River. It is situated at a position of 30° 13′ North and 89° 6′ West. Because of its position, the climate is milder than that of the mainland, with comparatively cool summers, warm winters, and moderate extremes of temperature. The island has a high percentage of sunshine, high relative

[1] The publication of extra illustrations in this article has been made possible by funds other than those of the Ecological Society of America.

humidity, and moderately heavy rainfall with uniform seasonal distribution. Frost is so rare that the growing season may be said to extend throughout the year.

The year 1931, in which most of our visits were made, was abnormally

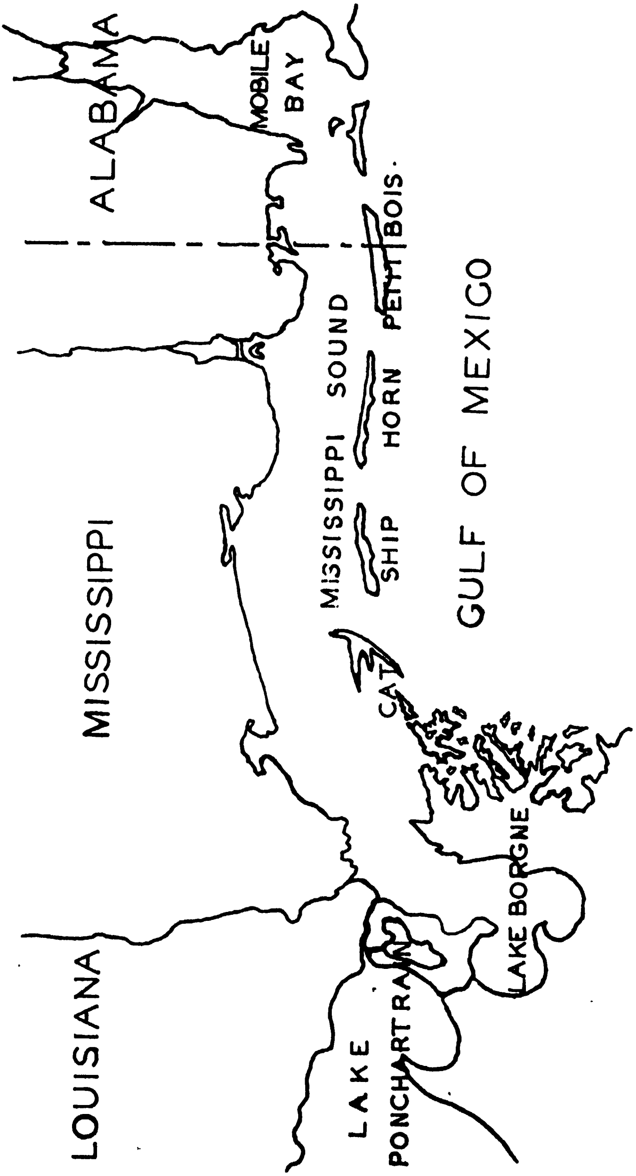

Fig. 1. Map showing the location of Cat Island.

warm during the last three months, and flowers bloomed profusely along the Mississippi coast until January, 1932. The mean annual temperature for Mississippi, 65.4° F., was nearly one degree above the normal. The stations

nearest to Cat Island where one may find climatological records are Bay St. Louis, some thirteen miles to the northwest, and Biloxi, about seventeen miles to the northeast. The mean annual temperature at these stations is nearly 4° F. higher than that for the state as a whole, and that of Cat Island is probably still higher. Although the precipitation was deficient from January to June, that of the state, 52.39 inches, was only 0.65 inches below normal for the entire year. At Bay St. Louis the rainfall was 14.73 inches higher than the mean annual for the state, and it is probable that Cat Island has a similar amount of precipitation.

The following tables are summarized from the reports of the United States Weather Bureau, furnished by the New Orleans office (tables I, II, III). They indicate clearly the favorable conditions for the growth of vegetation on this semi-tropical, continental island.

TABLE I. *General Meteorological Conditions at Stations near Cat Island*

	Elev. Feet	Mean Annual Temperature	Rainfall Inches	Clear Days	Partly Cloudy	Cloudy Days	Prevailing Wind
Bay St. Louis	39	68.2	67.81	180	116	69	South
Biloxi	41	68.6	62.36	—	—	—	Southeast

TABLE II. *Monthly and Annual Precipitation, 1931*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Bay St. Louis	5.98	4.18	6.14	2.59	3.56	3.49	12.00	8.97	1.90	4.82	2.56	11.62
Biloxi	4.93	3.14	6.83	2.72	3.10	2.92	8.93	10.38	3.74	4.20	1.39	10.08

TABLE III. *Monthly and Annual Mean Temperature, 1931*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Bay St. Louis	49.4	55.6	55.4	64.4	71.2	79.2	82.8	79.9	81.4	72.8	64.8	61.9	68.2
Biloxi	50.8	55.8	56.4	65.4	72.4	80.0	83.6	81.0	81.1	71.9	64.4	60.8	68.6

PHYSIOGRAPHIC FEATURES

Cat Island comprises an area of about seven square miles. It consists of two east-west axes attached at their eastern extremities to a long, narrow, north-south axis which is convex on the gulf side (fig. 2). The more northerly east-west spit is composed of two to sixteen sand ridges from four to ten feet in height and from a few feet to an eighth of a mile in width. These alternate with parallel depressions in which the floor is usually wet and often continuously covered with water, in some places to a depth of six feet. The other spit includes fewer and lower sand ridges and is mainly marshy in character.

The north-south spit is very different from either of the foregoing. It is

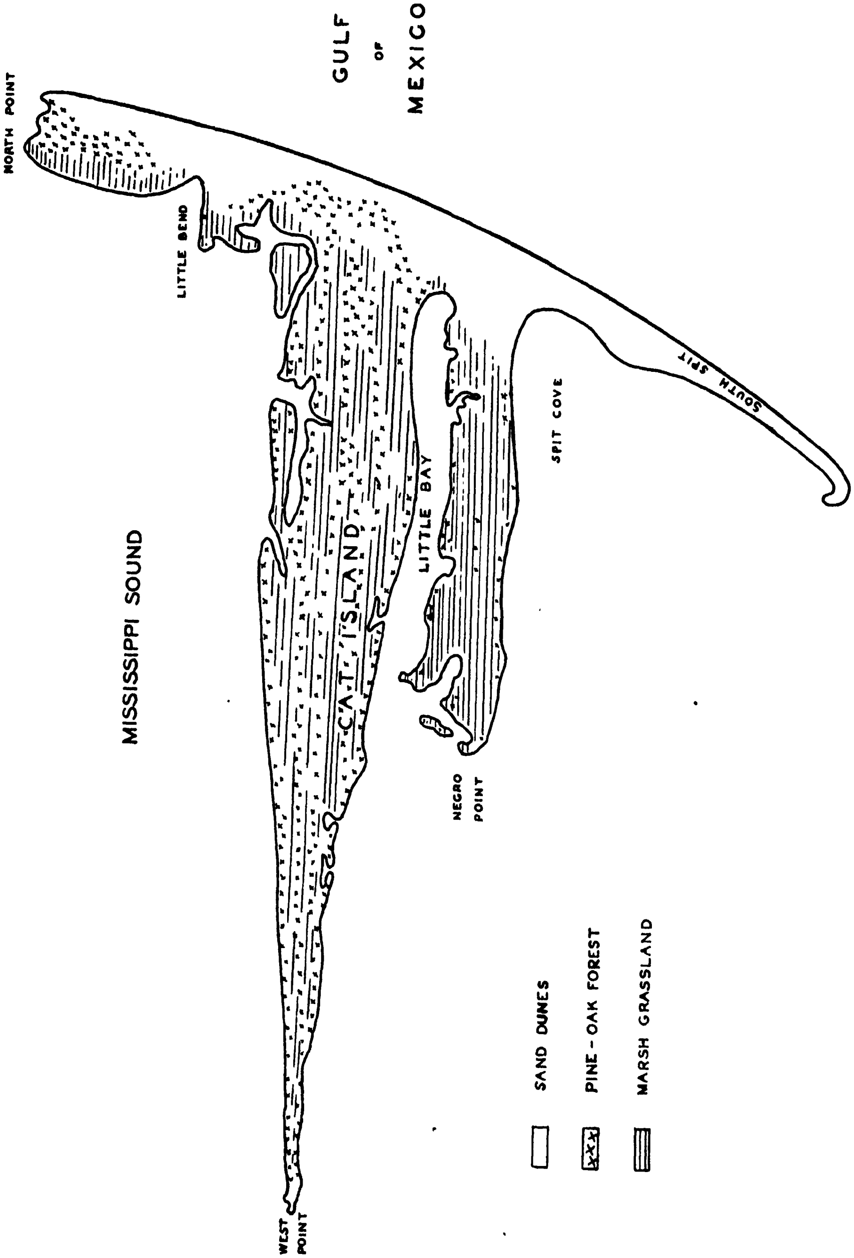

FIG. 2. Map showing the general physiographic and vegetational features of Cat Island.

composed of an eroding shoreline on the gulf side, various hillocks and dunes on the interior, and a zone of deposition on the western shoreline. On the gulf shoreline ghost forests of pine and oak extend more than a hundred feet into the gulf, and black, peaty soil, which could have been formed only in the marshes, is a conspicuous feature of the lower beach (fig. 3). The dunes

Fig. 3. Ghost forest and former marsh grassland (foreground) on the gulf shoreline at Cat Island.

Fig. 5. Saw-tooth palmettos with trunks, interesting curiosities on the sand dunes of Cat Island.

Fig. 4. A blow-out on the north-south spit showing xeric shrubs, and old stumps and living trees of the slash pine.

Fig. 6. Trees of the sand live oak with only the upper branches above the invading dunes.

vary from small haystack dunes a few feet in height to wandering, barren dunes of considerable extent and up to forty feet in height. They are composed of a glistening fine to medium white sand with a negligible quantity of organic matter and often very low water content. Throughout the dune area many blow-outs occur, and the Island is constantly changing in topography (fig. 4). At the junction of the east-west spits with the north-south axis the sand is advancing steadily over the marsh. This fact, together with the presence of peaty soil and ghost forests on the gulf shoreline, indicates that the island is gradually moving westward.

Vegetation

The east-west spits are well clothed with vegetation. The more southerly spit is given over almost entirely to brackish water marsh, but on the northernmost and larger spit the sand ridges are occupied by forests of slash pine and live oaks, the marshes being confined to the troughs between the ridges. On the other hand the north-south spit is scantily clad. The entire southern end of the spit for a distance of over two miles is a barren waste due to the fact that the waves wash over the low-lying sands in time of storm. On the tops and sides of the moving dunes there is little or no vegetation, and the active blow-outs are entirely devoid of plant life. The sand flats, in which sand movement is negligible, are being invaded by various rushes, sedges, and grasses, but in drier areas dunes are being built up mainly through the agency of the graceful and hardy sea oat. Only on the leeward side of the dunes are trees able to gain a foothold. Even here existence is precarious, since a moderate deposition of sand usually kills the slash pine and the saw-tooth palmetto (fig. 5). But the sand live oak, often with only the upper branches above the invading dunes, remains alive and apparently prosperous long after its compatriots have succumbed to the sand invasion (fig. 6).

In order to obtain a better conception of the various plant communities, the frequency index quadrat method, as developed by Raunkiaer (Gleason, '20), was employed. In each area a base line was established and the area divided into parallel strips at right angles to this line. Quadrats one square meter in size were located at intervals along the strips at a predetermined distance (3–7 paces) from each other, thus eliminating the personal factor of choice. Species were merely listed in each quadrat and marked by the number corresponding to the quadrat in which they occurred. At the conclusion of the count of species in the quadrats studied (25–100) the number and percentage of quadrats in which each species occurred was determined, the results being tabulated as frequency percentages. In addition, plants not actually included in the quadrats are added as a separate list.

The results of the quadrat studies were tested also by Raunkiaer's Law of Frequence (Kenoyer, '27). This was done by arranging the species in five classes, A (1–20), B (21–40), C (41–60), D (61–80), and E (81–100), according to the frequency groups in which they fell. In relatively stable

communities the relationship $A > B > C \gtreqless D < E$ usually obtains. The group A is usually the largest but contains the less important plants, whereas the E group ordinarily includes the dominant species.

In presenting the communities, those constituting the xerosere will be given first, together with a brief description of the climax forest. This will be followed by a discussion of the developmental communities in the fresh and brackish water areas, and at the end a chart showing the successional relation of all the communities will be presented. In the matter of nomenclature, Small's " Flora of the Southeastern United States " has been strictly followed.

Uniola Consocies

The dunes are rapidly colonized by the graceful and striking sea oat, *Uniola paniculata.* By its stout, running rhizomes deeply buried in the sand and its extensive network of fine roots, this hardy plant is able to bind the sand and cause dunes of considerable size to be formed (fig. 7). Associated with it, but altogether not equalling it in importance, are the following grasses, sedges, and forbs: *Andropogon maritimus, Cakile edentula, Cenchrus tribuloides, Chamaesyce ingalsii, Croton maritimus, Oenothera humifusa, Opuntia pes-corvi, Panicum repens, Physalis angustifolia, Poinsettia dentata,* and *Triplasis americana.*

Chrysoma-Helianthemum Associes

After the conditions become somewhat more mesic, especially where the area is protected from the strong winds from the gulf, a community of shrubs becomes established. The dominant shrubs are the shrubby goldenrod, *Chrysoma pauciflosculosa,* and the rock-rose, *Helianthemum arenicola,* although the attractive red calaminth, *Clinopodium coccineum,* and the cedar-like sand rosemary, *Ceratiola ericoides,* constitute a conspicuous element of the landscape. A glance at table IV indicates the relative importance of the plants and the

Table IV. *Frequency percentages of species in the Chrysoma-Helianthemum Associes, May 1, 1931*

Species	Common name	Frequency percentage
Helianthemum arenicola	Rockrose	94
Chrysoma pauciflosculosa	Shrubby goldenrod	91
Andropogon maritimus	Sand bluestem	42
Odontonychia corymbosa	Sand chickweed	38
Clinopodium coccineum	Red calaminth	32
Uniola paniculata	Sea oat	8
Panicum repens	Sea-beach grass	4
Cyperus lecontei	Sand coco-grass	2
Ceratiola ericoides	Sand rosemary	2
Pinus caribaea	Slash pine	1
Ilex vomitoria	Yaupon	1

paucity of the species. In addition to the quadrat list, the following occurred either in restricted areas or in lesser numbers: *Cakile edentula, Cenchrus tribuloides, Heterotheca subaxillaris, Muhlenbergia filipes, Opuntia pes-corvi,*

FIG. 7. Hay-stack dunes near the gulf shoreline held by the sea oat.

FIG. 9. A forest of live oak with an understory of the blue palmetto. This community probably constitutes the climax vegetation of the island.

FIG. 8. An open forest of slash pine with an understory of the saw-tooth palmetto against a background of white sand.

FIG. 10. A trough occupied by the Juncus consocies being filled with sand. The shrubby community along the border of the depression is Iva consocies.

Physalis angustifolia, Plantago sp., *Serenoa serrulata,* and *Solidago augustifolia.*

Pinus-Quercus Associes

In time the xeric shrub community, *Chrysoma-Helianthemum* associes, gives way to an open forest of slash pine, *Pinus caribaea,* or a forest composed of slash pine, sand live oak, *Quercus geminata,* and myrtle oak, *Quercus myrtifolia.* A conspicuous and often almost impenetrable understory of the saw-tooth palmetto, *Serenoa serrulata,* occurs throughout the stand (fig. 8). As is shown in table V, most of the species of the shrub community persist in

Table V. *Frequency percentages of species in Pinus-Quercus Associes, May 1, 1931*

Species	Common name	Frequency percentage
Andropogon maritimus	Sand bluestem	69
Capriola dactylon	Bermuda grass	55
Panicum repens	Sea-beach grass	55
Hydrocotyle bonariensis	Seaside pennywort	40
Pinus caribaea	Slash pine	28
Strophostyles helvola	Trailing wild bean	27
Xanthoxalis stricta	Upright wood-sorrel	21
Cyperus lecontei	Sand coco-grass	20
Adopogon carolinianus	Dwarf dandelion	18
Serenoa serrulata	Saw-tooth palmetto	18
Rubus trivialis	Dew-berry	15
Plantago sp.	Plantain	15
Linaria floridana	Toad-flax	14
Spermolepis divaricatus	Sand-parsley	14
Gnaphalium purpureum	Cat's paw	13
Crotalaria maritima	Rattle-box	12
Nothoscordium bivalve	False garlic	8
Helianthemum arenicola	Rock-rose	8
Solidago tenuifolia	Fragrant goldenrod	6
Festuca octoflora	Slender fescue-grass	4
Ascyrum hypericoides	St. Andrew's cross	4
Trifolium procumbens	Low hop-clover	3
Polygala nana	Milkwort	3
Quercus geminata	Sand live oak	2
Cnidosculus stimulosus	Tread-softly	2
Allium arenicola	Wild onion	1

the forest due to the open nature of the stand. Partly because of this there are no plants with a frequency of eighty-one or above, unless plants which arch over the quadrats be included in the quadrat lists.

In addition to the list on table V, the following species were less frequent, or were noted later in the season: *Aeschynomene viscidula, Aristida purpurascens, Bradburya virginiana, Carex tribuloides, Cenchrus tribuloides, Chamaesyce ingalsii, C. chiogenes, Chenopodium botrys, Croton maritimus, Erythrina herbacea, Eustachys petraea, Galium virgatum, Hypericum opacum, Pieris nitida, Pteridium aquilinum, Rynchospora glomerata, R. dodecandra, Sporobolus virginicus, Smilax lata, S. bona-nox, Trilisa odoratissima,* and *Yucca gloriosa.*

Quercus Consociation

In certain areas, presumably undisturbed for long periods by fire, a forest of live oak, *Quercus virginiana,* becomes established. This occurs only in a

few isolated spots and probably constitutes the climax vegetation of the island (fig. 9). The blue palmetto, *Sabal glabra,* occurs only in these spots and is a conspicuous understory in the live oak forest here just as on the mainland. Due to the small size of the areas, no frequency data were possible. A study of the following list indicates, however, its relationship with the live oak forest of the gulf coast: *Boehmeria cylindrica, Bumelia reclinata, Carduus spinosissimus, Eupatorium serotinum, Gnaphalium purpureum, Ilex vomitoria, Quercus virginiana, Sabal glabra, Schmaltzia copallina, Smilax bona-nox, Smilax lata, Fagara clava-herculis.*

Fresh Water Marshes

In the troughs between the sand ridges of the east-west spits the open water is invaded by various rushes, sedges, and grasses. Near the shorelines, especially where the troughs are connected by passes to the open sea, the water is salty or brackish, but near the middle of the spit it is almost entirely fresh.

The fresh or slightly brackish water marsh includes two communities, the saw-grass marsh occupying the wetter areas, and the black rush zone which is confined primarily to the borders of the depressions.

Cladium Consocies. The saw-grass, *Cladium effusum,* occurs in pure stand throughout most of this consocies and constitutes about ninety per cent of all the vegetation. Associated with it are the narrow-leaved cattail, *Typha angustifolia,* and the lance-leaved arrowhead, *Sagittaria lancifolia.* These plants are slowly invading the deeper water in which the bladderwort, *Utricularia vulgaris,* and the white water-lily, *Castalia odorata,* are the predominant plants.

Juncus Consocies. In this community the black rush, *Juncus roemerianus,* is the most important species, although the couch grass, *Spartina patens,* the sand rush, *Fimbristylis castanea,* and the gibbous panic-grass, *Sacciolepis gibba,* are present in considerable numbers. All of these species except *Sacciolepis gibba* are found in the brackish marshes. Of interest also in this community are the climbing milkweed, *Seutera palustris,* and the morning-glory, *Ipomoea speciosa.*

Brackish Marshes

The brackish or salt water marshes occupy a much greater area than the fresh water marsh. In the wetter and more salty portions the salt cane forms an extensive and compact community. But in progressively drier areas the salt grass and the black rush each form distinct vegetational units, and on the borders of the troughs a definite shrub zone occurs.

Spartina Consocies. This community is of peculiar interest in several respects. The salt cane, *Spartina stricta,* usually occurs in pure stand and constitutes about ninety-five per cent of the plants in this community. It occurs where the water table is usually above the soil surface, but tolerates great

extremes in salinity. It is about five feet tall in relatively fresh water, but less than one foot tall in very salty water. Only two other species have been found in this community and these are negligible in importance. Of the two, the salt grass, *Distichlis spicata*, and the black rush, *Juncus roemerianus*, the former is much more abundant.

Distichlis Consocies. This zone is a distinctive community characterized by the relatively small and attractive salt grass, *Distichlis spicata.* The plant forms pure stands over much of the area just above the salt cane where the mean water table is just about at the soil surface. It is in this community that the interesting glassworts, *Salicornia herbacea, S. ambigua,* and *Batis maritima,* find their best development.

Juncus Consocies. The *Juncus* consocies (the "Southern Juncaceous formation" of Mohr, '01) is the most extensive marsh community on the island (fig. 10). The predominant plant is the black rush or needle grass, *Juncus roemerianus,* which is characterized by stiff rhizomes and dark, sharp-pointed stems about three feet high, bearing near their tips compact clusters of reddish brown flowers. As co-dominants the couch grass, *Spartina patens,* and the sand rush, *Fimbristylis castanea,* may be of considerable importance over limited areas, but are greatly outnumbered by the black rush. Several other plants of low frequence also occur in this community, but are hardly worthy of mention here.

Iva Consocies. In the shrub zone the shrubby marsh elder, *Iva frutescens,* a composite, is the major dominant. Associated with it, but altogether not equalling it in importance are the buckbrush, *Baccharis halimifolia,* the wax myrtle, *Morella cerifera,* the winged bean, *Daubentonia longifolia,* and the coffee bean, *Sesban macrocarpa.*

Grass-Sedge Associes

Wherever the level of the marsh is aggraded above high tide level, especially by wind-blown sand, a grass-sedge meadow appears. Chief among the plants in this community are the sand bluestem, *Andropogon maritimus,* and the sand pennywort, *Centella repanda,* although a number of rushes and sedges are nearly as important. A good idea of the composition of the community may be gained from the frequency data in table VI obtained on May 1,

Table VI. *Frequency percentages of species in the Grass-sedge Associes, May 1, 1931*

Species	Common name	Frequency percentage
Andropogon maritimus	Sand bluestem	88
Centella repanda	Marsh pennywort	88
Fuirena scirpoidea	Spiked sedge	64
Juncus brachycarpus	Short-fruited sedge	58
Hydrocotyle bonariensis	Seaside pennywort	44
Xyris flabelliformis	Hard-head	28
Spartina patens	Couch grass	22
Lycopodium alopecuroides	Fox-tail club moss	18
Drosera intermedia	Sundew	10
Cyperus lecontei	Sand coco-grass	6
Scirpus olneyi	Three-cornered rush	6
Solidago tenuifolia	Fragrant goldenrod	4
Pinus caribaea	Slash pine	4
Scleria ciliata	Hairy nut-rush	4

1931. Other less important plants or plants found later in the season include: *Boehmeria cylindrica, Carex tenuifolia, Cyperus plankii, Eclipta alba, Eleocharis arenicola, Eragrostis purshii, Fimbristylis castanea, Gratiola hispida, Hypoxis hirsuta, Juncus brachycarpus, Monniera monniera,* and *Phyla nodiflora.* When this habitat is left in an undisturbed condition, especially where protected from the strong winds of the gulf, it is eventually reclaimed by the pine-oak forest.

Cyperus Consocies

If the level of the marsh is raised about a foot above the water table by wind-blown sand, few of the grass-sedge meadow plants survive. The result is a very open community in which the conspicuous plants are the sand coco-grass, *Cyperus lecontei,* and the seaside pennywort, *Hydrocotyle bonariensis.* As in the more arid *Uniola* consocies of the dunes, this community includes relatively few species (table VII). The plants are of low stature and reproduce primarily by rhizomes. They are similar to sand dune plants in that the rhizomes accommodate themselves to the changing level of the soil surface. But if too much sand is added to the area occupied by the *Cyperus* consocies the water content of the habitat is lowered to an unfavorable degree and the plants are killed. The sand again begins to wander, hillocks and dunes are formed, and a new xerosere is initiated.

Table VII. *Frequency percentages of species in the Cyperus Consocies, July 9, 1932*

Species	Common name	Frequency percentage
Cyperus lecontei	Sand coco-grass	100
Hydrocotyle bonariensis	Seaside pennywort	82
Panicum repens	Sea-beach grass	52
Andropogon maritimus	Sand bluestem	32
Juncus dichotomus	Forked rush	32
Eragrostis purshii	Southern love-grass	16
Fuirena scirpoidea	Spiked sedge	16
Spartina patens	Couch grass	12
Chamaesyce ingalsii	Creeping spurge	12
Juncus brachycarpus	Short-fruited rush	8
Fimbristylis castanea	Sand rush	8
Panicum lanuginosum	Wooly panic-grass	4
Cyperus rotundus	Coco-grass	2

Successional Relations

The successional relations on the Island may be shown readily by means of a chart (fig. 11). As has been indicated, the more important controlling factors are the water content of the soil and the salinity of the soil water. Nevertheless, it is true that trees and shrubs find difficulty in getting established where exposed to the strong winds from the Gulf of Mexico. This fact is indicated in the chart by the lines leading from the *Juncus* consocies. If the aggraded area is exposed to the gulf winds a grass-sedge meadow appears which develops slowly, if at all, into a forested area, unless subsequently protected by the erection of new dunes between it and the open sea.

Successional relations of plants are often influenced by biotic factors. Even though the island is well removed from the mainland, there is considerable evidence of the influence of man. Many of the slash pine trees have been streaked for turpentine, and a still greater number show fire scars or charred bark. Since there are about three hundred cattle and sheep being pastured on the Island, the palatable forbs and grasses are at a decided disadvantage, and since grazing animals are especially fond of the sea oat, the

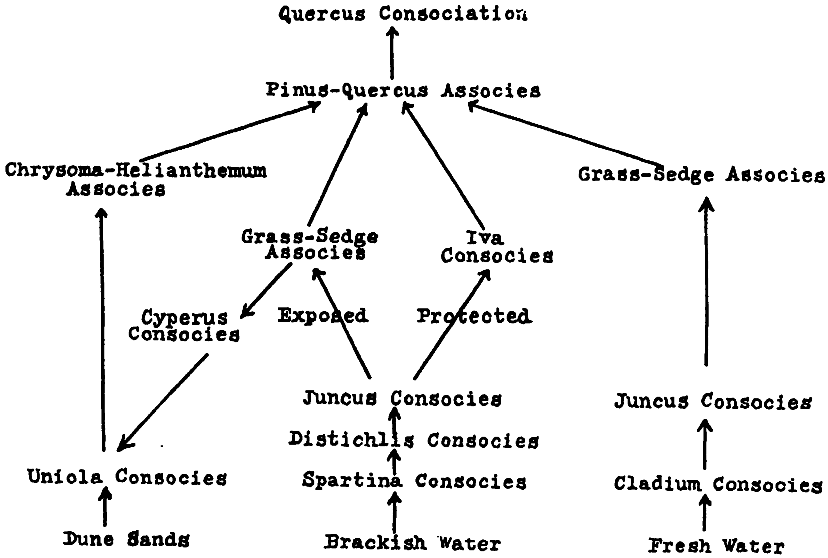

FIG. 11. Chart showing the successional relationships between the plant communities of Cat Island.[1]

colonization of the dunes is considerably impeded. In fact, both fire and grazing have been adverse factors in plant succession and have retarded, in large measure, the establishment of the live oak forest which appears to be the climax vegetation of the Island.

Physical Factors

Only meager data on physical factors have been obtained up to the present time, and these data represent the result of only one day's work (table VIII).

TABLE VIII. *Physical factor data for Cat Island communities, July 9, 1932*

Community	Water table Inches	Water content based on dry wt.	Organic matter	pH	Salt content of soil water
Uniola Consocies	—	1.0	0.07	6.9	—
Cyperus Consocies	—30	1.5	0.10	6.9	—
Pinus-Quercus Associes	—48	1.2	0.23	7.2	—
Grass-sedge Associes	—20	9.6	0.15	6.6	0.05
Distichlis Consocies	— 8	9.8	0.42	6.0	0.50
Spartina Consocies	+ 1	217.0	36.60	—	3.74

[1] Recent evidence indicates that the grass-sedge associes may be succeeded directly by the *Quercus* consociation.

As a result of low precipitation during late June and early July, the island was relatively dry on July 9, 1932, when these data were procured. The water contents in the first foot of soil on the sandy ridges were exceedingly low (1.0–1.5 per cent). In addition, the water table was about eight inches lower than usual. The relatively low water-holding capacity and sterility of the sandy soil is indicated by its low organic content. This, coupled with the fact that this soil is composed almost entirely of fine and medium sand (in equal proportions), is evidence of the difficulties offered to the ecesis of plants.

The salt content of the soil water in the bottom of the inter-ridge troughs varied from 3.74 per cent near the shoreline to 0.14 per cent on the interior. Although the outer depressions are occupied by brackish water species, the inner ones are given over primarily to the saw-grass, *Cladium effusum*. This is usually considered as a fresh water species, but the authors have never found it in a purely fresh water area. In the brackish water troughs the percentage of salt in the soil water decreases (from 3.74–0.05) with elevation. This relationship also has been found to obtain in other brackish water areas studied by the senior author.

Law of Frequence Studies

Studies on the degree of dispersal of plants in the arid communities on Cat Island show a surprising paucity of species (table IX). Only in the

Table IX. *Ratios of frequency groups in arid Cat Island communities*

	Frequency groups				
	A	B	C	D	E
Pinus-Quercus Associes	19	4	2	1	0
Chrysoma-Helianthemum Associes	6	2	1	0	2
Cyperus Consocies	8	2	1	0	2
Grass-sedge Associes	7	2	2	1	2
Average percentage ratios	63	16	9	3	9

pine-oak forest does the number of species approximate the number found elsewhere by Kenoyer ('27) and Hanson and Ball ('28); and this despite the fact that the more arid *Uniola* consocies was not included in our investigation.

In general, our data on the frequency groups check with the Law of Frequence in which A > B > C $\gtreqless$ D < E. An exception to this general rule is the data on the pine-oak forest in which group E is too low (table IX). This is due to the fact that the trees, which are dominant species, fell in groups A and B. When trees and shrubs which arch over the quadrats are listed in those quadrats, this difficulty is obviated, and these plants take their proper places in the higher frequency groups.

When the list of species found in similar frequency groups are added, and the results are expressed as percentages of the total number of plants listed in all four communities, the ratio 63, 16, 9, 3, 9 obtains. Raunkiaer's ratio (Hanson and Ball, '28) for a large number of European surveys was 53, 14,

9, 8, 16, and that of Kenoyer ('27) for fifty-one surveys in the region about the southern end of Lake Michigan was 69, 12, 6, 4, 9. It will be noted (table IX) that our ratios, although based on only four communities, agree rather closely with the foregoing ratios, especially with those of Kenoyer. And if the pine-oak survey be omitted, the ratio obtained (55, 16, 10, 3, 16) almost exactly coincides with that of Raunkiaer.

Summary

Cat Island is a semi-tropical continental island nine miles south of Gulfport, Mississippi. It consists of two east-west spits, composed of parallel sand ridges and depressions, attached at their eastern extremities to a north-south spit characterized by a changing sand dune topography.

The sand ridges of the east-west spits are clothed with a forest composed primarily of *Pinus caribaea* and *Quercus geminata*. The depressions near the shorelines are occupied by salt marsh, but the troughs toward the center are characterized by fresh water species.

In the fresh (really slightly brackish) water marsh the *Cladium* consocies constitutes most of the vegetation, the *Juncus* consocies being limited to the borders of the depressions.

In order of decreasing soil moisture, the brackish water communities include consocies of: *Spartina, Distichlis, Juncus*, and *Iva*. In time the *Iva* consocies is invaded by the *Pinus-Quercus* associes.

Wherever the area occupied by the *Juncus* consocies is aggraded by sand and exposed to the gulf winds, a grass-sedge associes appears, which develops slowly, if at all, into a forested area. If still more sand is added, most of the grass-sedge meadow plants are killed and the very open *Cyperus* consocies results.

The north-south spit is poorly clothed with vegetation. The entire southern end, for a distance of over two miles, is a barren waste, the moving dunes and blow-outs support little plant life, and much of the former vegetation has been killed by moving dunes.

In the xerosere the *Uniola* consocies is the first to obtain a foothold on the dry sands. This is followed by a xeric shrub community, the *Chrysoma-Helianthemum* associes, which is replaced in time by the *Pinus-Quercus* associes.

In isolated, favored spots throughout the Island, a climax forest of *Quercus virginiana* with an understory of *Sabal glabra* becomes established.

Of the physical factors, the water content of the soil, the salt content of the soil water, and the velocity of the gulf winds are the more important in determining the succession and distribution of the vegetation.

In addition, the biotic factors, through the processes of fire and grazing, have been adverse factors in plant succession.

Frequency studies revealed a surprising paucity of species in the xeric communities. Except for the *Pinus-Quercus* associes, our data on the Law of Frequence checked closely with that of other investigators.

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LENGTH OF LIFE SPAN AS A FACTOR IN REGULATING POPULATIONS [1]

Harley J. Van Cleave

University of Illinois

For a number of years the writer and students working in his laboratory have been studying some of the problems relating to the length of the life span for some of the common animals of the local fauna. In a number of instances, it has been observed that there are rather rigidly imposed limits to the normal length of life. The first species studied in this series of investigations was the blunt-nosed minnow (*Hyborhynchus notatus*). Within this species, males normally live to the age of approximately three years though the females are limited to about two years (Van Cleave and Markus, '29). Further studies, carried out more recently, on various invertebrates have demonstrated specific limits to the normal length of life for a number of species. There is no constant relation of the sexes in regard to relative length of life nor is there necessary agreement between species of closely related genera. In natural habitats adverse external conditions may result in accidental death of many individuals and thus obscure the facts relative to the presence of natural limitations of the life span. The present paper sets forth a comparison of two habitats for the same species of snail, in one of which 'natural death' is obscured when the population is analyzed because 'accidental death' is of such frequent occurrence.

Many of the treatises dealing with the regulation of numbers of individuals in populations in nature give the impression that conditions external to the organism establish the chief checks limiting numbers (Elton, '27, Chap. VIII). Climatic factors, relations in food chains, and epidemics are often more strongly emphasized than rate of reproduction, change in habits, length of life span, and other factors determined either by heredity or by physiological processes of the individual. Many writers have dealt primarily with organisms having either very brief or indefinite life duration. In instances where the individual life span is less than one year, its limitations are often readily correlated with and interpreted in terms of seasonal or climatic periodicity. A span extending over a series of years is not subject to such obvious periodicity correlated with seasonal changes and hence seems most readily interpretable as terminated by unspecified environmental factors when the true cause of death is unknown.

Recently, the attention of the writer has been directed to instances of what seem to be definite physiological limitations of life span covering more

[1] Contributions from the Zoological Laboratory of the University of Illinois, No. 443.

than a single year and hence not explainable in terms of limits induced by unfavorable climatic or seasonal states. However, in these instances, external conditions may intervene and secondarily impose a new set of controlling factors to reduce or even locally wipe out the population. Thus, in two different localities, the limits to the population may in one instance be determined by internal factors while in the other, external conditions may superimpose an entirely new set of limiting factors which may either modify the composition of the population or may even result in local eradication of the species.

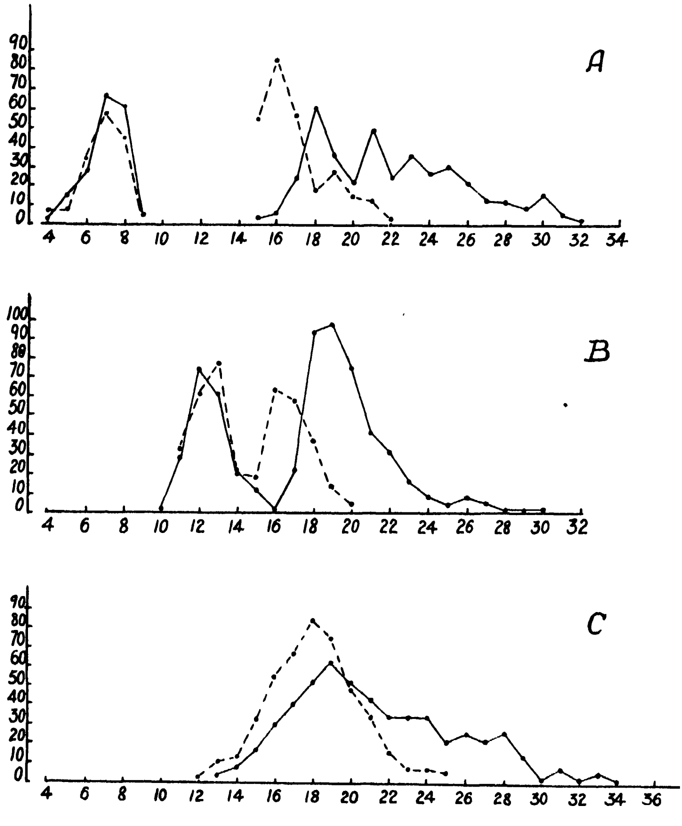

FIG. 1. Graphs showing progressive seasonal changes in height of shell of *Viviparus contectoides*, with particular reference to size or age groups for the two sexes. Numbers in actual population samples were corrected to a common basis to permit direct comparisons. Numerals on horizontal axis represent height of shell in mm.; on the vertical axis the number of individuals. Females in solid line, males in broken line.

FIG. A. Analysis of an early summer population sample, based on 334 individuals taken from the Erie Canal on June 17.

FIG. B. Analysis of a late summer population sample, based on 586 individuals taken from the Erie Canal on August 31.

FIG. C. Analysis of a late winter population sample of 629 individuals taken from the Illinois River on February 2.

A typical instance of a life span limited by hereditary or physiological control is that found in the large branchiferous snail, *Viviparus contectoides*. For this species, it has been found (Van Cleave and Lederer, '32) that the females live approximately three years though the males usually exceed an age of one year by not more than a few weeks. These facts have been ascertained by statistical analysis of periodic quantitative samples independently of their experimental demonstration for another species of the same genus by Annandale and Sewell ('21) working in India.

At birth, the males and females of *V. contectoides* are represented in the new generation in practically identical proportions (compare the two curves in fig. A, showing distribution of young females and males from 4 to 9 mm. in height). However, in the parent generation (the curves between 15 and 32 in fig. A) the females distinctly outnumber the males, due chiefly to the fact that the males normally die after living about one year while the population of females is cumulative, including individuals of the 1, 2, and 3 year age groups. Thus in the same sample, the proportions of the two sexes may show marked variations when different age groups are segregated.

By late summer or early fall (fig. B) the differential in growth rate between offspring and parent generations has resulted in the largest specimens of the new generation attaining a size equal to or exceeding that of the smallest individuals of the parent generation in both sexes. The two detached curves depicting separate generations in fig. A later become confluent for both sexes, but the curve representing females shows the cumulative effect of three generations living simultaneously. In contrast, the males in fig. B represent but two generations, with sharply defined limits in size. That these limits are age limits rather than merely growth limits is attested by the fact that there is no tendency what-so-ever toward piling up of numbers in the maximum size group. The growth curve for the parent generation of males shows the same abrupt drop at the upper size limits that was established by the individual differences in growth rate in the new-born generation.

By late winter (fig. C) before the onset of the parturition period, all of the males of the parent generation depicted in figs. A and B have died off, leaving only a single generation of males. The unimodal curve for males in fig. C with the mode at 18 mm., comprises the same group which had its mode at 7 mm. in early summer (fig. A) and had progressed to 13 mm. by late summer (fig. B). The curve for females in fig. C is composite, representing 1, 2, and 3 year groups. Thus, in late winter and early spring, just prior to the appearance of a new generation, there is present a set of conditions wholly different from those maintaining during the remainder of the year. Limitation of individual life span and especially the differential between the maximum age attainable by males and by females in this species produce seasonal facies to the population that could not exist in species having indefinite duration of life or having identical longevity for both sexes.

The conditions under which *Viviparus contectoides* lives are highly vari-

able. In connection with the above mentioned study on the life cycle, two stations were selected for field investigation of this species. One of these stations is the Erie Canal within the village of Durhamville, New York, and the other is along that stretch of the Illinois River above Peoria, Illinois, in the region known as Upper Peoria Lake. In these two stations, conditions of life and obvious causes of death for *Viviparus* are markedly different. In both localities, the young snails are used as food by some fishes, while the shells of snails more than a year old have attained a size and condition which renders them almost immune to the depredations of the ordinary snail-feeding fishes. According to Richardson ('28, p. 446) the channel catfish and the sheepshead are the only bottom-feeding fishes in fresh water capable of utilizing heavy-shelled snails as food. In the following discussion, the part played by snails in food chains will be disregarded, since conditions are approximately similar in the two habitats under consideration.

In the Erie Canal, conditions for the existence of *Viviparus contectoides* seem to be very stable and highly favorable for this species. Intimate field studies were carried on for three months through each of two summers. In that time, there was never any evidence of wholesale destruction of the snails. The littoral regions of the abandoned canal were so densely populated by living *Viviparus* that an area of three to six square yards usually sufficed for securing a sample of approximately 500 individuals. With each sample there were always a small number of dead shells of the same species, but these dead shells were almost invariably large and never exceeded the numbers which could be attributed to the toll of natural death imposed by the physiological limit to the duration of life which has been determined for this species. In other words, natural death seems to be a potent factor, if not the limiting factor, in determining the limits of the population of adult individuals of *Viviparus contectoides* in the Erie Canal.

In contrast, the same species is established in the Illinois River where environmental conditions are exceedingly severe as an accompaniment of pollution of the stream by sewage. As gill-breathers, snails of this genus are unable to survive conditions of oxygen shortage. In his intensive studies on the bottom fauna of the Illinois River, R. E. Richardson ('28, p. 404) has rated the Viviparidae as "cleaner-water species," placing them in the seventh, or final, major category of his groups of index organisms arranged in order of tolerance to pollution. During the periods of low water which marked the summers of 1930 and 1931 in the Illinois valley, the effects of pollution from up-stream became excessively severe (see Van Cleave, '31, p. 301–306). Organic sediments, settled out in the quiet waters impounded by dams and locks, were periodically swept farther down stream whenever the flow of the river was increased either by greater diversion from Lake Michigan or by rains. By this means, areas of heavy pollution were established in waters normally reasonably clean. Even the margins of Upper Peoria Lake, where relatively clean water exists under normal conditions, became

seriously contaminated and the colonies of *Viviparus* suffered local extermination. On February 2, 1931, Mr. Ludwig Lederer witnessed the results of a wholesale destruction of *Viviparus,* due presumably to recent contamination of a previously clean-water zone. On that date, the surface of the water over large areas was covered with floating snails, either dead or dying. A sample of 573 specimens picked from the surface of the lake, including 268 males and 305 females of which 194 bore marsupial young in the brood pouch. The sample was in every way a typical population of the species, representing all ages of both sexes in approximately normal proportions. Death had been the result of environmental factors in which pollution was unquestionably concerned, if not the sole causal agent. Wholesale blotting out of a colony in this manner stands in sharp contrast to normal restriction of a population through natural death of those individuals which have reached the physiological limit of life.

The snails killed by the polluted waters were washed ashore by wind action and currents. There they were piled in heaps forming practically unbroken ridges along the shore slightly above the season's high water mark. In the winter and spring of 1931, these shell heaps edged the west shore of Peoria Lake for a distance of at least six miles. While these heaps were predominantly composed of the dead shells of *Viviparus contectoides,* they contained minor representations of bivalves (both unionids and sphaeriids) and such snails as *Campeloma, Helisoma, Valvata,* and *Viviparus subpurpureus* in still smaller numbers. In February, 1931, the shell heaps edging the stream were, on the average, approximately thirty inches through the base and had a depth of about twelve inches. By May of the same year, the shells had become somewhat weathered and scattered but evidences of high rate of mortality were still glaringly present.

Under the variable conditions of pollution which characterize the Illinois River, pulses of relative abundance of *V. contectoides* are followed by periods verging onto complete extermination. Accidental death here becomes the most conspicuous factor limiting the population. This stands in sharp contrast with conditions in the Erie Canal described earlier in this paper, for there the same species lives under such uniformly favorable surroundings that pulses in relative abundance are practically wanting except at the climax of the parturition period. In the Erie Canal natural death, due to the physiological limit to the life span seems to be the chief check to numbers, hence the population is maintained at or near to the maximum, with only a relatively small proportion of the population suffering accidental death. In the Illinois River, local extermination is followed by the slow repopulation from remnants of colonies or by the still slower invasion from cleaner waters farther down stream, against the current.

In spite of the diversity in the conditions presented by the two habitats under consideration, *Viviparus* seems to undergo the same cycle in each. No compensatory adjustments have been observed. Distribution and rela-

tive abundance of the species are influenced and controlled by entirely different combinations of factors for the same species in the two localities. Population samples from the two stations, carefully selected to avoid inclusion of dead shells, when graphed on the basis of shell lengths, give specifically characteristic distribution. This fact provides evidence that in the species under consideration adverse environmental conditions exert no major selective influence disturbing the normal distribution of the sexes nor of size groups or age classes.

The influence of sharply incised age limits upon the form of a distribution curve is marked. Entire age groups drop out or enter the population in a relatively short period of time (compare figs. A and C). Natural death comes to a relatively large group of individuals in comparatively narrow limits of time after the specifically established age has been attained. This is especially true when there is a restricted breeding season. The limits of the distribution curve are sharply cut off for most seasons of the year, since there are no stragglers representing remnants of other generations to add confusion to the interpretation of the graphs. A predetermined length of life span is thus an obvious influence in determining the nature of populations, quite as significant as the environmental factors to which many writers have given undivided attention.

Summary

1. Length of life span may be an important factor in regulating the limits and composition of a natural population.

2. In *Viviparus contectoides*, the females live approximately three years. Graphs based on size of shell usually show the females falling into a multimodal distribution conforming to the age groups of three coexisting generations.

3. Males which live but little more than one year show bimodal distribution during most of the year but in late winter there is a single mode because the parent generation has died off.

4. Sex ratios are conspicuously altered by difference in natural life span of the two sexes.

5. In the Erie Canal at Durhamville, N. Y., the population of this snail is highly stable, death being due largely to 'natural' causes, chief of which is the inherent specific limit to the life span.

6. In the Illinois River, the same snail is subjected to adverse environmental conditions, due especially to sewage pollution, which at times wipe out entire colonies.

7. For the two habitats 'natural death' and 'accidental death' seem to play distinctive rôles in regulating the population.

8. The population is maintained at or near the maximum in the Erie Canal while pulses of relative abundance are followed by local extermination in the Illinois River.

9. Extermination rather than adjustment or selection seems to be the accompaniment of adverse environmental conditions superimposed upon the inherent tendency toward a specific limit to the life span.

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EVIDENCE OF THE RATE OF FOREST SUCCESSION ON STAR ISLAND, MINNESOTA [1]

Joseph Kittredge, Jr.

Lake States Forest Experiment Station

Star Island, with an area of 1200 acres in Cass Lake, offers an exceptional opportunity to reconstruct the forest succession where the vegetation has been least disturbed by human activities or by fire. It is situated about two and one half miles north of the town of Cass Lake on the boundary between Beltrami and Cass Counties, and forms part of the Chippewa National Forest.

The gently sloping upland is 15 to 25 feet above the lake level. Several depressions are occupied by swamps and the largest by Lake Windigo. Benches or terraces only a few feet above the water level, border the big lake and intervene between it and Lake Windigo (also called Lake Helen).

Geologically, the island forms part of the sandy outwash plain which surrounds Cass Lake, except on the northeast. The water-laid deposits deeply cover the bed rock which does not outcrop on the island or in the vicinity. Along the southwestern shore, the boulder clay which elsewhere does not occur near the surface, may be observed.

Cass Lake was visited by white men as early as 1806. Probably the lake was known to traders and explorers some years earlier. Star Island was named Colocaspi in 1820 by Schoolcraft. The northeast point of the island was the site of an Indian village. The significance of this early history is in the suggestion of probable fires on the island, either intentional or accidental, but always associated with the coming of the fur traders in the early part of the 19th century.

The trees have preserved in the fire scars the record of the more serious fires. The growth rings in the callouses of Norway and white pine indicate fires between 1808 and 1818 and in 1865, 1871 and 1872. Basswood sprouts and aspen suckers, 53 years old in 1924, represent the period since the fire in 1871 which killed the older trees from which the sprouts started. The jack pine, 100 years old in 1924, doubtless originated after a fire about 1824. Bits of charred wood in the forest floor similarly testify to the occurrence of fires. Apparently, however, no serious or extensive fire has burned over any large part of the island for more than 50 years.

Late in 1924, F. J. Alway pointed out that widely different forest types occurred on the island on the same soil type, mapped as Cass Lake fine sand

[1] The publication of an extra amount of tabular material in this article is made possible by funds other than those of the Ecological Society of America.

(Alway and McMiller, '33), and the author, cooperating with Alway, has studied the forest floor under the upland forest types (Alway, Kittredge and Methley, '33).

The principal upland forest types on Star Island are jack pine, Norway pine, white pine and sugar maple-basswood. These are now or were formerly widely distributed in the region, although repeated fires outside the National Forest boundaries have resulted in the replacement of much of the area of the Norway pine, white pine and sugar maple-basswood by jack pine or aspen.

On representative areas of the four principal types on the island, the larger trees were measured on 6 one-fourth or one-fifth acre plots and the smaller ones on 150 milacre quadrats.[2] Diameter measurements were made at a height of 4.5 feet above the ground. The examinations were made in November, 1924, October, 1929, May, 1930, and July, 1931.

Jack Pine Type

The jack pine quadrats were located on a 15 per cent slope with southern and western exposure. The old stand of jack pine, *Pinus banksiana*, in 1924 was 100 years old with average height of dominant trees of 86 feet, average diameter of 11 inches, number of trees per acre 6 inches and over in diameter 260, gross volume per acre 6,300 cubic feet or 27,000 board feet, mean annual growth per acre 63 cubic feet or 270 board feet. These figures indicate excellent growing conditions for jack pine. Its site index or average height of the dominant trees at 50 years, is 64 whereas the average for the region is 55 with a range from 42 to 73. The distribution of trees by species and size classes is shown in table I. Jack pine completely dominates in the over-wood. The larger jack pines, however, are dying each year and rarely is one found any where in the region more than 120 years old. Among the trees one inch or less in diameter, Norway pine, *Pinus resinosa*, is as numerous as jack and exceeds it in the classes from .5 to 4.5 feet high. Moreover, the small jack pines are noticeably spindling and few of them give promise of living to attain large size. White pine, *Pinus strobus*, also has 100 trees to the acre less than 4.5 feet high and is continuing to reproduce itself as shown by the presence of seedlings less than .5 foot high. In this area, the evidence indicates the occupation and dominance of a generation of jack pine for 100 years, the early part of a succeeding dominant stage of Norway pine which promises to replace the jack and a small beginning of a white pine stage which may eventually follow the Norway. The influence of the jack pine, on the lower vegetation, on the forest floor, and on the soil has extended over a period of 100 years, and may be expected to become negligible within another twenty years.

[2] A milacre is a square 6.6 feet on a side with an area of 0.001 acre or approximately 4 square meters.

TABLE I. *Jack Pine Type.*[1] *Number of trees per acre*

Size Class	Jack pine	Norway pine	White pine	Balsam fir	Paper birch	Red maple
Height in feet						
Less than .5			25	125		
- 1 -		75	50			25
- 3 -	25	325	25		125	25
4.5 and over	400	275			175	
Total	425	675	100	125	300	50
Diameter in inches						
1	675	475			200	
2	100	50			75	
3					25	
4					25	
5						
6						
7	4	4				
8	28					
9	32	8				
10	56					
11	52					
12	44	4				
13	24					
14	4					
Total over 6 inches	244	16				

[1] Data from a 100 year stand of jack pine along trail, one-eighth mile northwest of Lake Windigo. Tally of trees less than 1 inch in diameter on 40 milacres or 0.04 acre; of trees over 1 inch on one-fourth acre plot.

NORWAY PINE TYPE

In the sample areas of this type, over 95 per cent of the trees above 8 inches in diameter are Norway pine. A one-fourth acre plot has 200 trees to the acre between 10 and 22 inches in diameter. The average height of dominant trees is 98 feet, average diameter 17 inches, gross volume 13,000 cubic feet or 66,000 board feet per acre and the mean annual growth, 65 cubic feet or 330 board feet. The figures indicate a good site for Norway pine. The age of the over-wood is 200 years or a little more, and the trees are still vigorous and will probably live and maintain their dominance for at least 50 years longer. The distribution of sizes by species is shown in table II. The Norway pine is reproducing itself in moderate numbers, 228 per acre from one-half foot high to one-half inch in diameter, but white pine has 815 to the acre of corresponding size and an additional 515 to the acre in the 1 and 2 inch classes. The total number of white pines, all of them, except for an occasional one among the larger Norways, less than 3 inches in diameter, is 1459 to the acre. Obviously white pine predominates in the reproduction, and will probably dominate the next stage in the succession. The presence of a few red oaks, *Quercus borealis,* in the three-foot class may be noted

TABLE II. *Norway Pine Type.*[1] *Number of trees per acre*

Size Class	Norway pine	White pine	Red oak	Red maple	Paper birch	
Height in feet						
Less than .5		129				Larger trees 98% Norway pine, 2% white pine
- 1 -	43	43				
- 3 -	171	157	29			
4.5 and over	14	615		14		
Diameter in inches						
1		386			29	
2		129				
3					14	
Total	228	1459	29	14	43	
	On ¼ acre northwest of Lake Windigo					
8						
10	4					
12	16					
14	40					
16	60					
18	40					
20	28					
22	12					
Total	200 trees per acre over 8 inches in diameter					

[1] Reproduction on 70 milacres or 0.07 acre, north of telephone line and west of South Beach-Lake Windigo trail.

as a suggestion of the beginning of the successional stage which follows the white pine.

How long the Norway pine has been dominant is difficult to estimate. No evidence remains of a preceding jack pine stage. The present stand of relatively dense and even-aged Norway pine must have originated from the seed of a previous generation of Norway pines of cone-producing age. In places on the island there is now a dense stand of seedling Norway pines under the old trees. The influence of the Norway pine forest may therefore be supposed to have extended over a period of at least 300 years and probably much longer.

If the development of the forest of table II is projected forward until the large Norway pines are dead, a mixed forest of the present small white and Norway pines would naturally take its place. Good examples of this transition stage in its maturity are found on the east side of the island.

White Pine Type

One stand about 250 years old, contains 44 white and 56 Norway pines to the acre between 12 and 34 inches in diameter. The distribution of trees by sizes is shown in table III. The average diameter of the white pine is 28 inches and of the Norway, 22 inches, the average dominant height about 115 feet and the gross volume per acre for both species, 13,000 cubic feet or

72,000 board feet. The taller white pines are 125 feet high. The mean annual growth amounts to 52 cubic feet or 288 board feet per acre. This corresponds to a good site for Norway pine and a medium site for white pine. The age of this stand indicates that it represents a stage in the forest succession at least 220 years later than the foregoing Norway pine stand with white and Norway pine reproduction.

TABLE III. *Norway Pine-White Pine Transition.*[1] *Number of trees per acre over 8 inches in diameter*

Diameter Class	White pine	Norway pine
Inches		
10		4
12	4	
14	8	
16		4
18		8
20		16
22		12
24	4	8
26	8	4
28	8	4
30	8	
32		
34	4	
Total	44	60

[1] One-fourth acre plot on east side of the Island.

As the Norway pine gradually dies out, the white pine type is left as exemplified in table IV. In this stand, the larger white pines have been re-

TABLE IV. *White Pine Type.*[1] *Number of trees per acre*

Diameter Class	White pine	Norway pine	Sugar maple	Bass-wood	Paper birch	Red oak	Red maple
Inches							
Less than .5	500		200			100	
1							
2	4		20	20	8	4	4
3			20	4			
4			12		12		4
5			8		8		
6			8				
Total	504		268	24	28	104	8
8							
10							
12							
14							
16		4					
18							
20	4						
22	8						
24	4						
26	4						
Total	20	4 (trees over 8 inches in diameter).					

[1] Tally of trees less than 1 inch in diameter on 10 milacres or 0.01 acre; of trees over 1 inch on one-fourth acre plot, on east side.

duced by death to 20 and the Norway pines to 4 per acre. White pine is still reproducing but only 4 out of 504 seedlings to the acre have survived to grow above .5 foot in height. Norway pine is no longer represented in the reproduction. The incipient invasion of the next stage in the succession, the climax, is evident. Sugar maple, *Acer saccharum*, has 68 trees to the acre between 1.5 and 7 inches in diameter with a second generation of 200 less than .5 inch. Basswood, *Tilia americana*, and red oak are also represented but less abundantly.

White Pine-Maple-Basswood Transition

A still later stage in the transition from white pine to sugar maple-basswood occurs a short distance north of the foregoing stands. The figures are given in table V. Only an occassional very large white pine and more

Table V. *White Pine to Maple-Basswood Transition.*[1] *Number of trees per acre*

Size Class	White pine	Norway pine	Sugar maple	Basswood	Red oak	Paper birch	Large toothed aspen	Balsam fir	Red maple	Hop hornbeam
Height in feet										
Less than .5	50		8700		150	100		50	500	
– 1 –			1250	100	50	100			50	
– 3 –			350	50		200				
4.5 and over			200	50						
Total	50		10500	200	200	400		50	550	
Diameter in inches										
1				50				50		
2			55						15	25
3			45	5		10			15	5
4			15	5		20	5		30	
5			5	5		10				5
6						25			10	
7			5			10			5	
8			5			35				
9			5			5				
10			10				5			
12			10		5					
14			5		5					
31		5								
38	5									
42	5									
Total	10	5	160	65	10	115	10	50	75	35

[1] Area on east side, north of white pine-Norway pine transition. Tally of trees less than 1.5 inches diameter on 20 milacres or 0.02 acre and of trees over 1.5 inches on 0.2 acre.

rarely a Norway pine remain. Trees of these sizes, 31 to 42 inches, are doubtless over 300 years old. White pine reproduction is also reduced to 50 seedlings to the acre less than .5 foot in height and few of them are likely to persist. Sugar maple with smaller proportions of basswood and red oak already dominates except for the few veteran pines. The maple alone has 160 trees to the acre from 2 to 15 inches in diameter and 10,500 less than .5 inch.

The white pine stage, as far as the evidence on Star Island goes, is limited to one long generation. It starts under the Norway pine and before its maturity and decadence in 250 to 350 years, the sugar maple and its associates have established themselves so firmly that the white pine no longer regenerates successfully. The period of occupation and influence of the white pine may therefore be placed at not less than 250 years.

Maple-Basswood Type

Finally, the climax forest dominated by sugar maple and basswood is also represented on the island on the bench northeast of Lake Windigo. The stand per acre in trees 2 to 16 inches in diameter contains 144 sugar maples, 272 basswoods, and 96 American elms, *Ulmus americana*. The distribution by species and sizes appears in table VI. The average diameter is about 7

Table VI. *Sugar Maple-Basswood Type.*[1] *Number of trees per acre*

Diameter Class	Sugar maple	Bass-wood	Elm	Red oak	Hop hornbeam
Inches					
Less than .5	17300		100	100	
1	100				
2	20	8			
3	16	12			
4	12	48	16		
5	32	32	16		4
6	16	48	12		
7	8	28	12		
8		16	12		
9	8	8	8		
10		16	4		
11	4	12	12		
12	8	16			
13	8	4			
14	8	16			
15		8			
16	4				
Total 2 inches and over	144	272	92		4

[1] Area on bench northeast of Lake Windigo. Tally of trees 1 inch and less on 10 milacres or 0.01 acre; of trees 2 inches and over on .25 acre.

inches, average dominant height 57 feet and age 60 years. This represents a poor site for sugar maple-basswood. The large proportion of basswood may be ascribed to the fire which destroyed the previous generation and enabled the basswood, by its high sprouting capacity, to gain in the competition with the poorly sprouting maple. In the absence of fire, however, the maple tends to increase its numbers by its abundant seedling reproduction. This tendency is evident in the seedlings in the present stand, 17,300 sugar maples per acre, 100 elms, 100 red oaks, and no basswood on the quadrats counted. The

maintenance of the climax forest and the increasing dominance of the sugar maple seem assured.

The history of this area prior to the fire 60 years ago cannot be reconstructed with certainty. A few large fire-scarred maples and red oaks are remnants of the former stand and the large diameters of the circles formed by the groups of basswoods, which started as sprouts around fire-killed snags, now gone, testify to the size of the previous generation. Evidently the earlier stand had much the same composition as to species as the present one but was much older, probably 200 years or more. No trace of pines remains on this area. This confirms further the supposition of a long occupation, probably more than 300 years by the maple-basswood climax. The red oak provides the only and a rather uncertain measure of the time which has elapsed since the pine disappeared from this area. Red oak tends to be eliminated by the maple and basswood. Only one or two relicts of the species are left which are over 30 inches in diameter, probably over 250 years old. Very large and healthy red oaks doubtless over 200 years old, remain on an area where the pine has disappeared. And in the forest where only a few old pines persist (table V), the red oaks have only reached diameters of 12 to 14 inches corresponding to ages of not over 100 years. These trees would live 100 to 200 years after the pines were gone. If only one long-lived generation of red oak is assumed, that alone would account for probably 200 years of occupation by the present maple-basswood forest since the disappearance of the last of the pines and their influence. If the red oak persisted for two generations, as it might, the period would be more than doubled.

Subordinate Vegetation

The shrubby and herbaceous vegetation associated with the different forest types contributes its influence with that of the trees to the soil and soil forming processes. The enumeration and cover of the different species are given in table VII. The figures for cover are estimates according to a scale in which 4 represents $\frac{1}{2}$ to $\frac{1}{4}$ of the area covered; 3, $\frac{1}{4}$ to $\frac{1}{8}$; 2, $\frac{1}{8}$ to $\frac{1}{16}$; 1, $\frac{1}{16}$ to $\frac{1}{32}$; and t, less than $\frac{1}{32}$ of the area. This is the Hult-Sernander scale modified to restrict their class 1 to a lower limit of $\frac{1}{32}$ and to include an additional class below $\frac{1}{32}$. Many of the species are found in all four types. Many others, although they were observed only in one or two of the types on Star Island, also occur in the others as indicated by much more extensive observations in the region. There are, however, certain ones which are almost exclusively associated with specific types and may, therefore, be assumed to contribute to or result from any specific features of the soils in those types.

For the jack and Norway pine types, *Arctostaphylos uva-ursi, Gaultheria procumbens, Vaccinium pennsylvanicum, Chimaphila umbellata, Melampyrum lineare* and *Lycopodium complanatum* are quite typical and are rarely if ever found with the sugar maple-basswood or with white pine at the stage when

TABLE VII. *Shrubby and herbaceous vegetation*[1] *of the Forest Types on Star Island, July 19, 1931, with amount of cover*

Species	Jack pine	Norway pine	White pine	Maple-basswood
Arctostaphylos uva-ursi	3	t		
Vaccinium pennsylvanicum	3	2	t	
Lycopodium complanatum	2	1		
Maianthemum canadense	2	1	1	t
Anemone quinquefolia	1	t	t	t
Linnaea borealis	1	1	t	
Oryzopsis asperifolia	1	1	t	t
Vaccinium canadense	1	t		
Apocynum androsaemifolium	t			
Campanula rotundifolia	t			
Aster laevis	t			
Chimaphila umbellata	t			
Comandra umbellata	t			
Cornus canadensis	t	t		
Cornus rugosa	t	t	t	t
Cypripedium acaule	t			
Danthonia spicata	t			
Epilobium angustifolium	t		t	
Lathyrus ochroleucus	t	t		
Lonicera hirsuta	t		t	
Melampyrum lineare	t	t		
Prunus pennsylvanica	t			
Amelanchier sp.	t	t		
Aralia nudicaulis	1	3	1	1
Prunus virginiana		2	1	t
Pteris aquilina	1	2		
Amelanchier sanguinea		1	t	t
Fragaria americana	t	1		
Gaultheria procumbens	t	1		
Rosa blanda	t	1	t	
Diervilla lonicera		1	t	
Galium boreale		t		
Lonicera canadensis		t	t	t
Oryzopsis pungens		t		
Polygala paucifolia		t		
Pyrola secunda		t	t	
Pyrola americana		t		
Rhus toxicodendron		t	t	
Salix humilis		t		
Acer spicatum			4	t
Corylus rostrata	t	3	3	1
Carex sp.	t	t	1	
Streptopus longipes			1	
Clintonia borealis	t		1	
Trientalis americana	t	t	1	
Galium triflorum			1	
Lycopodium obscurum var. *dendroideum*			1	
Aster macrophyllus			t	
Lonicera glaucescens			t	t
Rubus strigosus var. *canadensis*			t	
Ribes cynosbati			t	t
Sambucus racemosa			t	
Uvularia grandiflora			t	4
Carex sp.				3
Smilacina racemosa				2
Viburnum affine var. *hypomalacum*			t	1
Polygonatum biflorum			t	1

TABLE VII. *Continued*

Species	Jack pine	Norway pine	White pine	Maple-basswood
Actaea rubra f. *neglecta*				t
Botrychium virginianum				t
Parthenocissus vitacea				t
Smilacina stellata				t
Viola sp.				t
Cornus alternifolia				t
Celastrus scandens				t
Smilax herbacea				t
Asplenium filix-femina				t
Xanthoxylum americanum				t

[1] Scientific names for the woody plants, from Rosendahl and Butters' "Trees and Shrubs of Minnesota" and for others, from Gray's "New Manual of Botany" ed. 7, are used throughout.

those species are invading. It may be noted that the first four species belong to the Ericaceae whose members are definitely associated with acid soils and in Europe, considered to contribute to the formation of raw humus and podsol profiles. Quite different in character from the foregoing species but typical of the maple-basswood forest are *Uvularia grandiflora, Actaea rubra* f. *neglecta, Cornus alternifolia, Polygonatum biflorum, Celastrus scandens, Smilax herbacea,* and *Asplenium filix-femina.*

The white pine type, the intermediate stage in the succession, has no species of undergrowth which do not also occur commonly either with the Norway pine on the one side or with the maple-basswood on the other. The *Galium triflorum, Lycopodium obscurum* var. *dendroideum* and *Rubus strigosus* var. *canadensis* shown in table VII only in the white pine type, are known to be associated frequently with maple and basswood in other localities, and consequently they cannot be considered typical of the white pine type.

THE FOREST SUCCESSION AS A WHOLE

The successional changes in forest composition are summarized in table VIII. The trees over 8 inches in diameter represent the dominant element of the community in each stage, those between 1 and 8 inches, the established invaders of the succeeding stage, and those less than 1 inch, the precursors of a generation which will not become dominant in 100 years or more. By following the changes in the different species and size classes from stage to stage, the evidence of the progression of dominants, the invasions, the transitions and the consummation of the whole succession become clear.

The reconstruction of the periods of the life cycles of the dominants and thereby the estimation of the rate of the forest succession, also provides a measure of at least the minimum periods during which the reactions on the forest floor have been operative. This has particular interest in connection with the properties of the forest floor which are discussed in a separate paper

TABLE VIII. *Summary of the Successional Changes in Forest Composition. Number of trees per acre by species*

Forest Type	Diam. group inches	Jack pine	Norway pine	White pine	Red oak	Paper birch	Sugar maple	Basswood	Elm	Others
Jack pine	Over 8.5	212	12							
	1 - 8	807	519			325				
	Under 1	425	675	100		300				125
Norway pine	Over 8.5		200							
	1 - 8			515		43				
	Under 1		228	944	29					14
White pine	Over 8.5		4	20						
	1 - 8			4	4	28	68	24		8
	Under 1			500	100		200			
White pine-maple-basswood transition	Over 8.5		5	10	10	5	30			
	1 - 8					110	130	65		160
	Under 1			50	200	400	10500	200		600
Maple-basswood	Over 8.5						40	80	24	
	1 - 8						204	192	68	4
	Under 1				100		17300		100	

(Alway, Kittredge and Methley, '33). Summarizing the successional time table, the jack pine influence extended over 100 years, the Norway pine, 300 years or more, and the white pine, 250 years or more, a total of at least 650 years of occupation by the pine types. The influence of the sugar maple-basswood forest in turn has lasted during 100 years of transition from the pine type and at least 200 years since the disappearance of the pine, a total of something over 300 years. These typical examples of the stages in the forest succession have developed in not less than the indicated minimum periods of time on the same soil type, classified as Cass Lake fine sand.

Why the forest succession has reached widely different stages in different parts of the island on the same mineral soil can only be a matter of conjecture. Differences in the frequency or intensity of forest fires, which probably occurred before those of which records are now obtainable, would afford a plausible explanation. This possibility is strengthened by the fact that the maple-basswood type which would develop only in the absence of fires, is to the northeast of Lake Windigo and on the points of the island where water areas have minimized the chances and effects of fires fanned by the prevailing southwest winds of the fire seasons.

SUMMARY

The forests of Star Island afford excellent examples of the four stages in the succession from jack pine to Norway pine, from Norway pine to white pine, and from white pine to sugar maple-basswood. The evidence of the transitions between each two stages is exceptionally complete and leaves no doubt that the entire succession from jack pine to the sugar maple-basswood climax would be consummated in a sufficient period of time.

The minimum periods of occupation by the four stages are for jack pine 100 years, for Norway pine 300 years, and for white pine 250, a total of at least 650 years before the sugar maple-basswood climax would become dominant after the establishment of the pioneer jack pine forest.

Each of the transitions is now progressing on the same soil type and the whole forest succession has undoubtedly been completed on this soil in the areas of the present sugar maple-basswood climax.

This single soil type is at one and the same time an excellent site for jack and Norway pine, a good site for white pine, and a rather poor site for maple-basswood, indicating that the reaction on soil productivity has not kept pace with the vegetational succession.

The subordinate vegetation exhibits changes in floristic composition and cover corresponding to the stages in the forest succession but few species are exclusively typical of any one stage.

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CYPRESS BUTTRESSES AND KNEES IN RELATION TO WATER AND AIR

Herman Kurz

Florida State College for Women

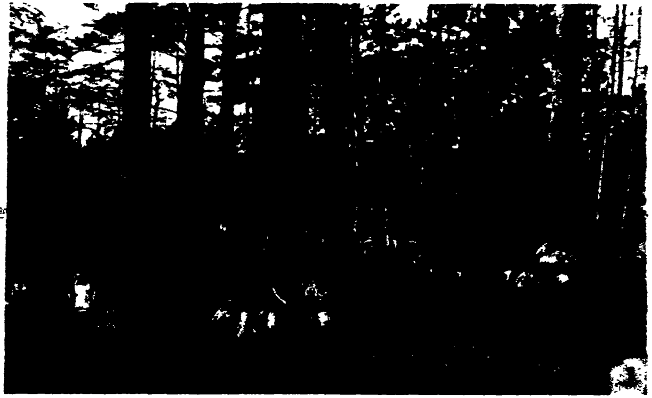
Delzie Demaree

Stanford University, California

Enlarged bases of certain trees growing in swamps are very familiar to botanists and naturalists. The spectacular buttresses of cypress offer classical examples of such responses to water. Ordinarily, however, a cypress buttress is not seen in its entirety for the greater part of it is masked by the water, especially in the deeper lakes and ponds. The form, therefore, that the bases assume from the water level downward, unless the water is unusually calm and clear, can only be conjectured by the explorer boating about casually during high-water periods. The prolonged drouths of 1927 and 1931 gave the senior author excellent opportunities to explore dry-footed a number of ponds and lakes in middle northern Florida. Figures 1, 2, and 3 show three distinctive types of buttresses developed by pond cypress, *Taxodium ascendens* Brongn., when growing in as many different habitats.

The first type is very low, wide, and truncated. Harper has described ('02) and published photographs ('05) taken in Coffee County, Georgia, of bases so flat that one can walk around the tree on them. He associates these with shallow water of rather constant level. Mattoon ('15) also illustrates this type of "low broad base" and correlates it with shallow, non-alluvial swamps. The second type of buttress is plainly conical. In conversation with the senior author, Harper has stated that this form is associated with habitats which fluctuate actively and over a considerable range of depth. The third type appearing like gigantic bottles, previously described by Kurz ('30), is found in ponds or lakes attaining much greater depths than either the habitats of the shallow or conical-based trees.

All three of the foregoing types suggest the influence of water level fluctuation in fashioning them; but they hardly indicated, much less proved, the importance of a second factor in buttress development. The junior author's studies of Reelfoot Lake make quite certain the nature of the second factor. Reelfoot Lake, lying just east of the Mississippi in northwestern Tennessee, was formed by land subsidence during the famous New Madrid earthquake of 1811–12. Fuller ('12) has given a comprehensive report on this geological phenomenon. Nelson ('24) gives an admirable popular account of the history of Reelfoot Lake. The catastrophic subsidence referred to above



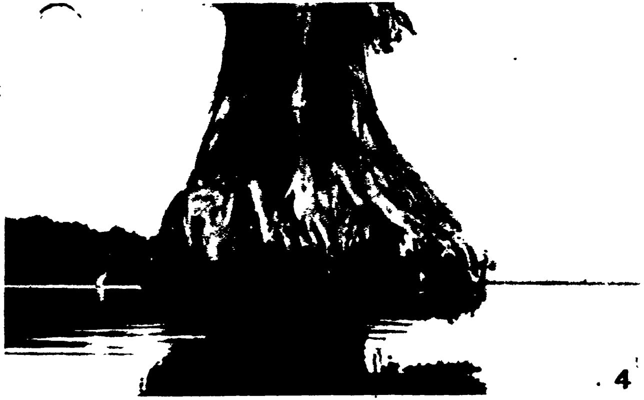


FIG. 1. Shallow buttress of *Taxodium ascendens* Brongn. about ten miles south Marianna, Florida.

FIG. 3. Bottle buttress of *Taxodium ascendens* Brongn. near Tallahassee, Florida.

FIG. 2. Cone buttress of *Taxodium ascendens* Brongn. about three miles west of Ponce De Leon, Florida.

FIG. 4. Hanging buttress of *Taxodium distichum* (L.) Richard. Reelfoot Lake, Tennessee.

submerged the trunks of large numbers of bald cypress, *Taxodium distichum* (L.) Richard. A new water level then encircled and bathed the trees considerably higher up the trunks. Just how much higher depended upon the local topography of the lake floor. Fuller ('12), Nelson ('24), Demaree ('32), and undoubtedly others observed that many cypress trees perished in the deeper waters while those left in shallower waters after the subsidence survived. " Rivers or other bodies of water which have an average seasonal fluctuation of more than ten or twelve feet " are considered fatal to cypress by Harper (p. 760, '12). Recently Demaree ('32) has shown experimentally that even a cypress may be drowned. However, in this paper we are primarily concerned with the living relics antedating the earthquake referred to above.

In 1929 and 1930 the water level fell appreciably below normal. The survivors of the earthquake now unmasked presented an amazing sight. Contrary to all expectation, their buttresses did not extend to the lake floor but terminated abruptly just below the usual water level. In figure 4 is a buttress hanging high and dry like a bell! In many instances the diameter of these butts exceeded the remainder of the stem above and below by two or three feet. Amazing is the fact that the growth in diameter of these cypress trunks has been as normal below the range of ordinary water fluctuation as it has been above. Our explanation is that the segment of the trunk above the bell is always aerated but seldom wet; and, therefore, not buttressed. The segment below the normal water level is nearly always soaked but rarely aerated; consequently, it is also without buttress. Between these two segments, however, is a limited third segment above or below which the water level seldom rises or falls; therefore, some particular zone of this third segment, because of splashing and soaking, is nearly always in contact with water plus air. Thus it seems to us that buttress development is a response to the simultaneous presence of water and air (presumably oxygen). This conclusion is supported by the very fact that there is such a thing as a cylindrical or bottle-shaped butt. Were water alone the factor all buttresses would necessarily be widest at the base; for no matter what the rate or range of fluctuation or what the depth of water, the lowest portion of a buttress would be subjected to the greatest amount of hydration and would therefore be the widest.

It would seem therefore that the form of any particular buttress will depend upon the frequency as well as the duration with which its various horizons are subjected at once to water and air. In fact, the profile of the buttress itself may be used to express in the form of a curve the relative total time that its various stories have been subjected to aerated water or hydrated air. In figure 5 a cone-shaped buttress has been turned to the left 90° and the upper profile used as a curve. If we assume that the growth in diameter at any air-watered zone of the buttress is practically uniform throughout the growing season, we may reason as follows. At *A* the amount of air-watering is negligible and the diameter of the trunk is therefore normal. The diameter at *C*

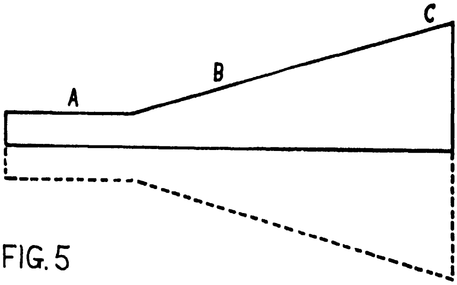


FIG. 5

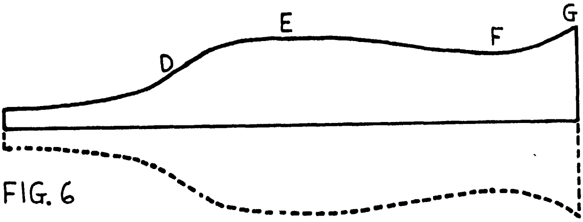


FIG. 6

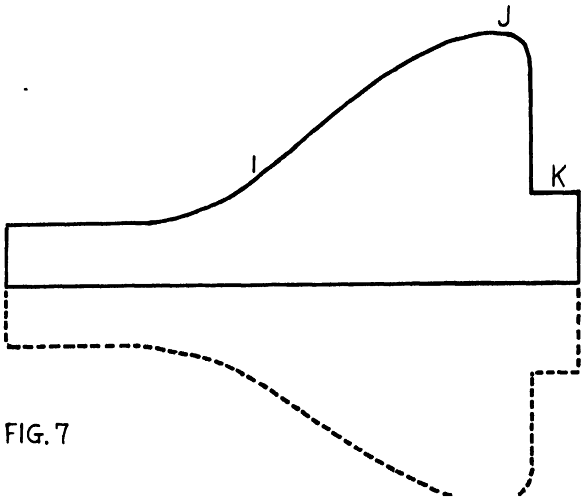


FIG. 7

FIG. 5. Profile of a cone-shaped buttress used to express in the form of a curve the relative total time its various horizons have been subjected simultaneously to water and air.

FIG. 6. Profile of bottle buttress used to express in the form of a curve the relative total time its various horizons have been subjected simultaneously to water and air.

FIG. 7. Profile of a bell-shaped buttress used to express in the form of a curve the relative total time its various horizons have been simultaneously subjected to water and air.

is twice that at *B*; that means then that the horizon *C* has been played upon simultaneously by water plus air for a sum total of time which is about twice as long as the total time that horizon *B* has been subjected to water plus air.

Similarly, if the bottle buttress be turned to the left 90° we get the curve shown in figure 6. At *D* the total time that a given horizon is air-watered increases rapidly toward the right until a maximum is indicated at *E*. From here the air-watering runs about uniform until *F* is reached where a slight diminution is indicated. At *G* there is a slight flare again. This flare may be due in part to a greater air-watering and in part to the root system which begins here (fig. 6).

The most illuminating curve, however, is the one presented by the Reelfoot Lake buttress (fig. 7). At *I* is seen essentially what was shown at the corresponding level at *D* in figure 6. But the impressive skewing of the curve at *J* is due to the fact that here the trunk is seldom at once wet and aerated. The very slight rise of the curve from *K* on indicates abundant watering but very little aerating.

Using swollen cypress bases as their own curves we can also readily interpret the history of shallow and other types of buttresses in terms of water-level fluctuation and water-air visitations. Moreover, these buttresses when exposed or visible may themselves be used as curves to express relative stability or fluctuation of water level as well as changes in the depth of bodies of water.

Cypress Knees

In the literature cypress knees have commonly been considered special organs of aeration. Mattoon ('15) reviews a number of theories that have been advanced concerning the utility of such extraordinary growth forms. However, it is especially difficult to reconcile the aeration hypothesis with the fact that cypresses of the deeper waters are devoid of knees. The reader will notice the absence of such organs in figure 3. Yet in this pond the water frequently reaches a depth of eight, ten and twelve feet. Cypress knees are also conspicuously absent in the deeper waters of Reelfoot Lake. Still, they are common in the shallower margins, and in the shallow pockets of water in the drained areas of the " Sunken Lands " of the same region. The authors of this paper think that knees are not a reaction to the paucity of oxygen but like buttresses rather a response to water plus air. Such explanation disregards the well-known aerations theory, as well it might, and conforms nicely with Harper's statement (p. 760, '12), that " its trunk usually emerges from the ground just about low-water mark and its enlarged base and ' knees ' are generally believed to reach up approximately to the average level of high water " or, with Mattoon's assertion (p. 26, '15), that " knees occur mostly where water covers the surface for long periods and their height corresponds rather closely to the average high-water level for the locality."

Summary

Cypress buttresses are considered a response to water plus air. The buttresses themselves may be used as curves to express the total water-air exposure to which the various levels of the buttresses have been subjected.

Knees, like buttresses, are considered reactions to water plus air exposure.

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OBSERVATIONS ON DROUGHT INJURY IN MINNESOTA FORESTS

HARDY L. SHIRLEY

Lake States Forest Experiment Station

The summer of 1930 was one of deficient rainfall over a large part of the middle western United States. Great damage was done to native vegetation as well as to farm crops. Heavy losses to forest plantations occurred in both Michigan and Minnesota. Plantations in Minnesota, established even as early as 1925 and 1926, sustained losses of from 30 to 50 per cent.

In view of the deficit in precipitation, such losses are no greater than might have been expected. The average annual precipitation for the Chippewa National Forest, Minnesota, on which this study was concentrated, is about 25 inches, of which the greater part falls during the summer months. The average deficit for weather stations located in the vicinity of the forest was 5.15 inches while for two stations actually on the forest it was 7.0 and 10.9 inches. During July and August precipitation was two and three inches, respectively, below the normal for these months. Drought injury to vegetation was most pronounced in August. Herbaceous vegetation died and some of the hardwood trees, particularly aspen and birch, shed a number of their leaves. Succulent vegetation was so scarce during September that rabbits readily ate pine and spruce seedlings which were planted in the field.

Even swamp forests suffered from lack of moisture. Ordinarily, it is assumed that swamps or bogs are free from damage by drought, but this does not apply to the large areas of comparatively flat swampy land in northern Minnesota. Most of these swamps are quite shallow, and, although the water table is usually at the surface, during periods of prolonged drought it may drop below the level of accumulated peat to the mineral soil. When the swamp does get dry, it presents even more xerophytic conditions than upland. This condition was approximated on a black spruce swamp drained for experimental purposes in 1926. Practically all the shrubs, Laborador tea, cranberry, pale laurel, and bog rosemary died down to the ground. Sphagnum moss became almost powder dry. The surface of the swamp became so arid that 25 per cent of the trees under one inch in diameter breast high were wiped out. Only one spruce seedling of 1930 origin was found alive in 1931 as contrasted with 44 for the previous year. Losses were most heavy in the seedlings less than six inches in height and progressively decreased with increasing height.

No particular damage to mature trees was noticeable anywhere on the Forest, but young growth suffered severely. Where forest reproduction was

abundant on uplands, large brown patches with occasional green trees interspersed could be observed. Injury was generally well distributed but tended to be more severe on knolls and other exposed situations. Grading for a road caused the death of jack pine seedlings five feet high as far back as 20 feet from the escarpment.

Not all of the losses to forest reproduction can be attributed to the action of drought alone. Of 21 dead seedlings of Norway pine, *Pinus resinosa*, examined in August of 1930, 20 showed signs of root damage, which was evidently caused by white grubs, the larvae of May beetles, *Phyllophaga* spp. Of the losses incurred in national forest plantations, 50 per cent were attributed directly to drought, 38 per cent to the action of white grubs, and 12 per cent to other causes. Undoubtedly, many conifers suffer root injury from white grubs, but during summers of normal precipitation the damage is not sufficiently severe to result in their death. Grub injury is seldom noticeable on trees which have attained a height of more than two or three feet.

Considerable local damage was done to reproduction through the action of pocket gophers. These animals cut the pine roots in their runways and in some cases may cause the loss of seedlings 10 or more feet in height.

Sources of Information

On August 22, 1930, a brief study was made of the plants injured and killed by drought on four permanent sample plots in jack pine, *Pinus banksiana,* which had been subjected to different degrees of cutting. Each species of plant encountered was recorded as thrifty, poor, or dead, depending on its condition at that time. It was expected to extend the observations to other areas, particularly aspen stands, but circumstances rendered this impossible.

Annual records of the numbers of seedlings on definite quadrats are kept for sample plots in jack pine, aspen, and black spruce, *Picea mariana,* stands. An estimate of the losses due to drought is given by the difference between the spring counts of 1930 and 1931. The losses in aspen were insignificant compared with those in the pine and spruce stands.

To supplement this material, a series of strip surveys were run across pine areas which had suffered drought losses. Each strip was 6.6 feet wide and the tallies were kept separately for each 66 feet of strip. A total of 312 separate 0.01 acre tallies were thus taken. Every tree was tallied by species, height class, and whether alive or dead. Most of the trees tallied were jack pine. The height classes used with corresponding ages for jack pine are given in table I.

TABLE I. *Height classes and age for jack pine*

Height classes (Feet)	0–1	1.1–2.0	2.1–4.0	4.1–8.0	8.1 +
Age in years median	2	3	5	8	12

Drought Losses in Pine Forests

Pine, on the Chippewa National Forest, occupies a fine sandy soil of glacio-fluvial origin. This is usually underlain by layers of coarser sands alternating with fine sand and clay at depths below two or three feet. The soil was quite moist at and below the clay layers, but the upper two feet became extremely dry during the summer.

The greater part of the material on drought losses was obtained in pine forests. The amount of loss was found to vary inversely with height of seedlings, density of seedlings, density of brush cover and density of upper canopy.

Height and Drought Losses

In all the counts made, not a single pine seedling of 1930 origin could be found alive in the spring of 1931 except a few on artificially prepared seed spots. Quite a number of natural seedlings were observed in the early summer of 1930, but by late August practically all of them had died.

In tables II and III, the drought losses are given for different height classes. In all cases the shorter trees suffered the greatest losses. This, of course, is to be expected since the trees in the lower height classes are generally younger and their roots have not penetrated to the deeper soil levels. Only a few of the trees over 8 feet in height were killed by the drought.

Table II. *The effect of a jack pine overstory on drought losses to Norway, white, and jack pine reproduction of different heights*

Species	Height class (Feet)	No. of trees observed	Density of pine stands Per cent of normal basal area 93	58	45	15	Total
			Per cent of trees dead				
Norway pine	0– .5	14	20	33	0	100	29
	.5–1.5	20	0	33	0	75	20
	1.5–4.5	35	8	0	—	55	20
	4.5 +	7	0	0	—	0	0
All heights		76	7	14	0	55	20
White pine	0– .5	6	0	0	0	100	17
	.5–1.5	14	0	0	33	83	43
	1.5–4.5	9	0	0	0	50	11
	4.5 +	3	—	0	—	0	0
All heights		32	0	0	17	64	25
Jack pine	0– .5	97	43	58	60	75	60
	.5–1.5	158	28	20	30	76	42
	1.5–4.5	163	27	16	11	40	28
	4.5 +	27	0	0	0	10	4
All heights		445	28	29	35	54	39
All species	0– .5	117	29	50	56	79	55
	.5–1.5	192	21	20	28	77	40
	1.5–4.5	207	21	11	10	42	26
	4.5 +	37	0	0	0	7	3
All heights		553	21	25	33	55	35

TABLE III. *Effect of size and density of stocking on drought loss to jack pine*

Density class	Mean density per acre	No. of trees observed	Per cent dead by height class 0–1	1–2	2–4	4–8	8+	All heights
0–5,000	1,460	3,270	70	42	22	5	4	35
5,001–10,000	8,800	970	59	40	20	7	0	31
Over 10,000	18,900	1,514	25	39	9	1.3	0.2	3.7

EFFECT OF DENSITY OF REPRODUCTION ON DROUGHT LOSSES

The drought losses occurring in stands with different densities of stocking are given in table III. For stocking of less than 10,000 trees per acre, the losses were about 34 per cent, while for areas having more than 10,000 trees per acre the losses were only about one-tenth as great. For the stands included in this study, it is apparent that increasing density caused a decrease in drought losses within the limits of stocking encountered. Since this observation is at variance with the current conceptions of the effect of density on drought losses, it merits some attempt at explanation.

Three factors were observed in the field which probably played important rôles in effecting this result. The one which was first noticed was the differences in soil and exposure. The poorer and drier situations naturally suffered greater losses from drought, and these areas, for the same reason, supported less dense stands of pine reproduction. This was especially noticeable on south facing slopes. Another factor which undoubtedly had an important influence was the shrubby and herbaceous vegetation which grew interspersed with the pine. Stands having more than 10,000 trees per acre had already closed, and thus set up forest conditions similar to those in older aged stands. The ground was completely shaded and practically all lesser vegetation was crowded out, leaving the soil covered with typical needle litter. This was not true of the less dense stands. In these the trees grew as isolated individuals surrounded by dense sod and brush. It is quite likely that this sod drew much more heavily upon the soil moisture than did the tree seedlings. The sod and brush were themselves killed back to the surface of the soil in many places.

Perhaps of equal importance is the protection which the densely growing trees afforded one another against the desiccating action of dry winds and intense insolation. Pearson ('24) has shown that coniferous seedlings are capable of reducing the amount of water transpired to an almost negligible amount when the soil becomes critically dry. During such periods, protection against the sun and wind might enable many plants to survive that otherwise would perish.

For the stands in question, the beneficial effects of crowding appear to be of much more importance for survival than the deleterious effects of mutual competition above and below ground. It is unfortunate from the standpoint of the forester that the poorly stocked stands, which can least afford drought losses, should suffer most severely.

Brush Cover and Drought Losses

A few of the survey strips were run through areas occupied by brush species of varying densities. The most prevalent species were prairie willow, beaked and American hazelnut, Inland Jersey tea, and fire cherry. There was also a rather heavy sod of grass and sedge where the brush was not too dense. The density of brush cover on each 0.01 acre strip was estimated in 5 per cent classes. The results are summarized by 20 per cent classes in table IV. As brush cover increased the survival during drought also increased. In this case the brush was not sufficiently high to form a canopy over the pine, but was evidently valuable in providing some shade and protection from dry winds.

Table IV. *The influence of brush cover on the drought losses to jack pine*

Brush cover density in per cent	No. of trees observed	Per cent dead
0–20	149	10.1
21–40	163	9.8
41–60	125	4.8
61–80	78	1.3
81–100	26	0

Influence of Upper Canopy on Drought Losses

The drought losses to reproduction under canopies of different densities are shown in table II. The heavier losses occurred in the plots subjected to the heaviest degree of cutting.

Further evidence of the ameliorating effect of an upper canopy during periods of drought is furnished by a study made on August 22, 1930, of the herbaceous vegetation on the same plots. The results, given in table V, are in substantial agreement with those obtained from counts of coniferous reproduction. A similar set of plots in jack pine, located on the Superior National Forest, showed greatest losses to reproduction on the plot subjected to the heaviest cutting. Conifers suffered much more severely from drought than aspen and birch, which are much less valuable for forestry purposes.

Table V. *Effect of type of cutting in mature jack pine on drought injury to undergrowth*

Type of cutting	Per cent of normal basal area left	Total no. of species observed	Thrifty	Poor	Dead
			Per cent		
Heavy	15	45	15	38	47
Moderate	45	47	21	45	34
Light	58	47	23	43	34
Uncut	93	50	46	48	6

Relative Drought Resistance of Different Species

From table II it is seen that jack pine suffered greater losses from drought than either Norway or white pine, *Pinus strobus*. This is based on trees of the same height. Jack pine has a much more rapid juvenile growth than either Norway or white pine, hence had the comparison been made for trees of the same age the results might have been reversed. Jack pine suffered relatively less loss on the heavily cut plot than the other pines.

Drought Losses in Relation to Root Competition

Toumey ('26, '28, '31), Barr ('30), Craib ('29), Fabricius ('27, '29) and Fricke ('04) have stressed the great importance of root competition in determining the survival and growth of plants under forest canopies. They have shown that, in general, during the dry seasons the soil moisture is lower under forest canopies than in the open. Furthermore, they have conclusively demonstrated, for certain localities, that, if the tree roots entering a definite area are all severed, the ground cover on this area becomes much more luxuriant and rapid growth sets in.

Because the large trees tend to deplete soil moisture more rapidly than less massive forms of vegetation, it is natural to infer that, during periods of drought, the forest presents less favorable conditions for plant survival than unforested areas.

On the basis of the data presented herein, such an inference does not appear to hold true for the pine forests of Minnesota. While the soil moisture in the forest apparently did fall below that outside, and in some cases actually may have fallen below the wilting coefficient, the plants were protected against excessive transpiration losses by the shade of the large trees. Apparently the beneficial effects of shade in reducing the transpiration losses more than offset the unfavorable effects of root competition.

An interesting speculation is presented by the work of Breazeale ('30) and Magistad and Breazeale ('29). They have found that plant roots may actually exude water into the dry upper layers of soil if the plant has a tap root extending into moist layers. Whether tree roots by this means could raise appreciably the moisture content of the upper soil layer during dry periods is still a matter for conjecture.

In any case, low soil moisture even at the wilting coefficient, if of short duration, is not necessarily fatal to all plants unless it is accompanied by excessive transpiration.

The results of these observations tend to emphasize the importance of partial cutting, particularly on areas likely to suffer from drought. On rocky ridges or light sandy soils, it is of paramount importance to maintain adequate shade until the reproduction is advanced sufficiently to withstand high transpiration. Likewise in planting, survival is likely to be much better if some shade is present. An overstory provides excellent shade but, where this cannot be had, a light brush cover may be valuable.

While shade may often be of considerable value in enhancing early survival, it must be used with caution, for after the trees are once well started, shade is seldom beneficial. A vigorous-growing so-called nurse crop too often crowds out or greatly stunts the growth of the crop desired.

Summary

A survey of losses due to the 1930 drought in Minnesota was made in swamp and pine forests. Losses in the swamp were particularly heavy for young black spruce seedlings rooted in the upper layers of moss. No losses were observed in older trees.

Drought losses in pine forests decreased in severity with increasing height and density of reproduction, and with increasing density of brush cover and upper canopy.

The unfavorable effect of root competition of older trees was more than offset by the beneficial effects of their shade.

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THE OCCURRENCE OF GUTIERREZIA SAROTHRAE ON BOUTELOUA ERIOPODA RANGES IN SOUTHERN NEW MEXICO

R. S. Campbell and E. H. Bomberger[1]

Southwestern Forest and Range Experiment Station

Bouteloua eriopoda Torr. (black grama) is characteristic of the desert plains association described by Weaver and Clements ('29), and extends from southwestern Texas through southern New Mexico, Arizona and northern Mexico. This grass, if not depleted, is the most abundant and valuable forage species on the well-drained sandy or gravelly soils of dry mesas in the region, especially in southern New Mexico.

Jardine and Forsling ('22) have shown that continued overgrazing of *Bouteloua eriopoda* range leads to deterioration of the valuable grasses and the establishment of *Gutierrezia* spp. (snakeweed or broomweed), accompanied by reductions in grazing capacity and loss of soil stability. The ultimate result of continued injudicious grazing may be a transformation of the *Bouteloua* range to the *Prosopis* (mesquite) sand dune scrub association. Periodic drought is partly responsible for the deterioration, because of the wide spacing of plants resulting from low rainfall, and the facility with which the range is overgrazed when inadequate precipitation causes poor forage production.

Many ranchmen believe that *Gutierrezia* will crowd out the valuable forage grasses on the range. This opinion results from failure to recognize overutilization and ignoring the fact that on grass ranges, the unpalatable *Gutierrezia* plants are subject to little foliage removal by cattle, while the palatable grasses, when overutilized, sometimes are eaten to within a half inch of the soil surface.

In order to determine the trend of *Gutierrezia* occurrence in the *Bouteloua eriopoda* association, and to establish its significance in plant succession, a study of the problem was initiated.

The work upon which this paper is based was done near Las Cruces, New Mexico, on the Jornada Experimental Range, a branch of the Southwestern Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture.

Methods of Investigation

In July, 1924, three one by three meter quadrats were established in a *Bouteloua eriopoda* association supporting a fairly dense stand of *Gutierrezia*

[1] Acknowledgment is due J. D. Schoeller, who established this study in 1924, and collected the data until 1927. Constructive criticism of the report was given by several members of the Forest Service.

sarothrae (Pursh) Britt. & Rusby.[2] The quadrats were located within an area one hundred yards in diameter, according to the following scheme:

Quadrat 1. A stand of young *G. sarothrae* seedlings had become established, but *B. eriopoda* was still dominant.

Quadrat 2. *B. eriopoda* was decidedly dominant, but *G. sarothrae* seedlings were present.

Quadrat 3. *G. sarothrae* appeared to be dominant, with several mature plants and numerous seedlings, but *B. eriopoda* made up 38.9 per cent of the quadrat tuft area.

The vegetation on the quadrats was mapped in the autumn of each year, in 1924 by the strap method, and from 1925 to 1930, inclusive, by the chartograph method, as described by McGinnies ('30). *Bouteloua* tufts and the *Gutierrezia* plants were mapped at one inch above the soil surface, and were compiled in square centimeters. The extreme diameter and height of each *Gutierrezia* specimen were measured and recorded. Supplementary notes on vegetative and biotic conditions were made for the area in which the plots were located, each time the quadrats were mapped. These notes included a careful ocular estimate of the plant density and composition on the area, based upon the grazing reconnaissance method developed by the Forest Service, as described by Campbell ('31).

The degrees of grazing use were recorded in June each year as a part of the regular grazing capacity project. These data show in percentages the volume of range feed used by grazing animals and are based upon the growth requirements of *B. eriopoda.*

Factors Influencing the Vegetation

In order to understand the conditions under which the study was made, it is necessary to present available measures of the habitat, which may be grouped conveniently under climatic, physiographic, and biotic factors.

Climatic Factors

The following data show the monthly mean maximum and minimum air temperatures at the Jornada range headquarters about 6 miles northeast of the study area, from 1914 to 1930, in degrees Fahrenheit:

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Max.	55.3	62.5	67.2	74.0	83.4	94.7	93.0	91.8	86.8	76.7	63.9	53.1
Min.	21.2	26.4	31.1	39.1	46.7	56.2	63.9	61.8	55.1	42.0	28.9	22.2

Temperatures are favorable for growth from April into October, but rainfall limits the growing season during most years to the three months of July, August and September, as shown by the following monthly precipitation

[2] In this report, *G. sarothrae* includes *G. longifolia* Greene, *G. tenuis* Greene, and tentatively *G. juncea* Greene, fide Dr. S. F. Blake, Bureau of Plant Industry, United States Department of Agriculture.

means, expressed in inches, at the Jornada range headquarters from 1914 to 1930, inclusive:

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
0.28	0.32	0.48	0.16	0.64	0.28	1.82	1.73	1.16	1.09	0.42	0.64

Occasionally the growing season may continue into early October, but low temperatures usually limit growth after October 15. During the summer, the mean evaporation from a free water surface is approximately 12 inches or less per month, and wind movement is well under 3000 miles per month, as measured at Elephant Butte Dam (Linney, '17–'30), a station reasonably comparable to the Jornada range. During the spring, however, the peak of unfavorable growth conditions is reached, with low rainfall, mean evaporation well over 12 inches per month during May and June, and with mean wind movement from 3000 to 3500 miles per month during the entire spring period.

Physiographic Factors

The quadrats were located in a *B. eriopoda* association on soil which is a grayish to pale reddish, fine to medium sand, with a comparatively high percentage of gravel, and characterized by a loose, pervious structure. At variable depths from 2 to 6 feet, the surface layer of sand and gravel is underlain by a hard, whitish, calcareous caliche. In general, it is a porous dry soil, with a structure unfavorable for moisture retention.

The site of the study is approximately 4200 feet above sea level on the gently undulating, featureless plain of the Jornada mesa.

Biotic Influences

The biotic community on the range, as Taylor ('30) points out, includes not only the forage plants and livestock, but all the plants and native animals. The flora, domestic livestock, and certain fauna will be considered with the experimental results, but the great majority of native fauna must be given only passing attention, largely because so little is known concerning the various species and their food requirements.

In a partial census of the fauna associated with *Yucca elata*, a member of the *Bouteloua* association, Campbell and Keller ('32) listed 39 insect species, 2 reptiles and 3 mammals. Little is known of the interrelationships of these and many other animals to each other and to the vegetation. Although it is known that such genera as *Lepus*, *Sylvilagus*, *Dipodomys*, and *Neotoma* either consume or destroy large quantities of plant material, the available data are insufficient to determine whether the value of such animals in building up soil fertility compensates for their removal of forage. On the study area the rodent population was not excessive at any time between 1924 and 1930, but insects clearly affected the *Gutierrezia* in 1925 and 1927.

THE BOUTELOUA ERIOPODA ASSOCIATION

The plant density and composition of the *B. eriopoda* association may vary considerably between different sites and different stages of development on the same area. A representative association, after two or three years of favorable rainfall and conservative grazing supports a plant density of approximately 0.35, of which 60 to 70 per cent is *B. eriopoda* (fig. 1). The sand dropseed grasses, *Sporobolus cryptandrus* and *S. flexuosus,* and three awn grasses, *Aristida pansa* and *A. purpurea,* make up about 15 per cent of the stand. *Triodia pulchella* and the annual grasses *B. barbata* and *A. ad-*

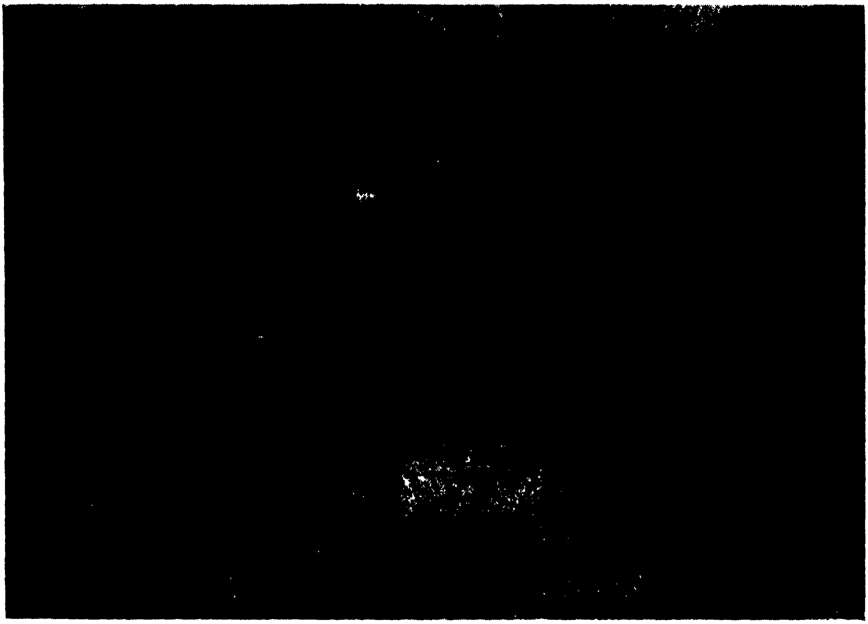

FIG. 1. General view of a *Bouteloua eriopoda* association with Quadrat 2 in the foreground, 1931.

scensionis are present, along with the following forbs, listed in order of their abundance: *Croton corymbulosus, Lesquerella fendleri, Solanum elaeagnifolium, Dithyraea wislizeni, Cassia bauhinioides, Psilotrophe tagetinae,* and others. Of the shrubs, *Gutierrezia sarothrae* constitutes from 5 to 10 per cent of the plant cover; with *Yucca elata, Prosopis glandulosa, Ephedra trifurca* and others contributing 4 or 5 per cent. Although all of these species must be considered with the *Bouteloua* association on large areas, only *B. eriopoda* and *G. sarothrae* will be considered in detail, since they were the only species present on the quadrats throughout the period of study, except for occasional forbs or annual grasses.

Bouteloua eriopoda

This is a perennial, tufted short grass with branching, whitish woolly culms which may vary from 4 to 36 inches in length (fig. 2). Many of the stems are creeping stolons, and produce buds at the nodes, which may take root and grow into new tufts. The plant has a finely divided, well developed root system, mainly in the upppermost 10 inches of soil.

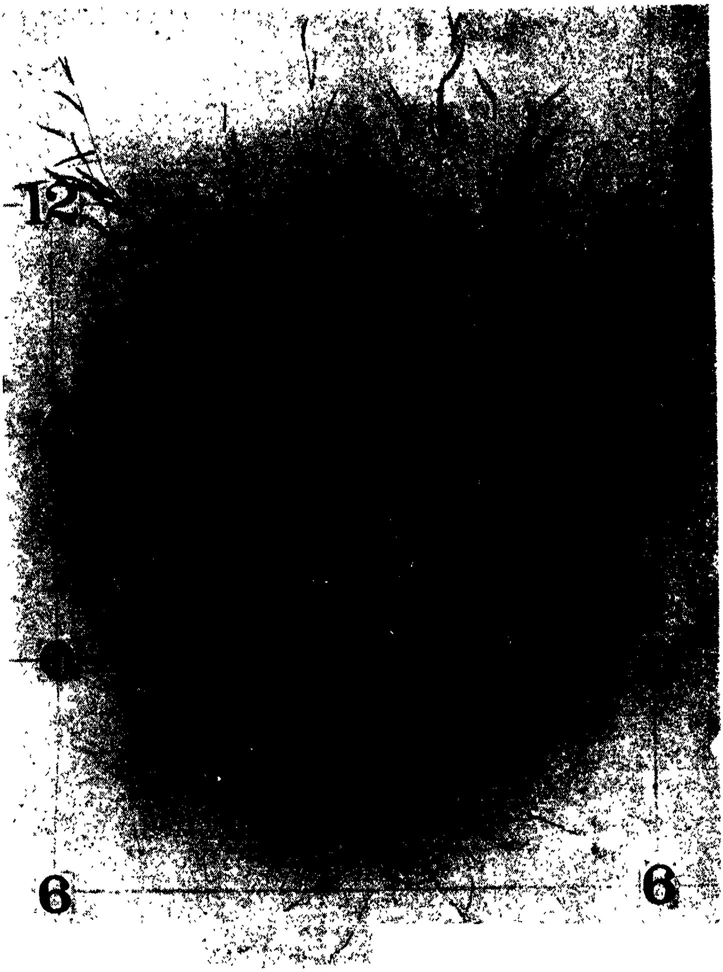

Fig. 2. A tuft of *Bouteloua eriopoda,* showing the character of root system, flower stalks and stolons with rooting buds at the nodes. Dimensions in inches.

The principal spread of the *Bouteloua* comes from lateral extension of individual tufts, as a result of new peripheral stems. Nelson [3] has shown

[3] **Nelson, Enoch W.** 1930. The influence of precipitation and grazing upon black grama range. (MS.)

that increase in tuft area by this method may amount to 190 per cent in favorable growing years. The production of new plants from rooted buds on the stolons also is an important method of vegetative reproduction, mainly during years with above-average summer rainfall.

It reproduces very sparingly from seed in southern New Mexico, largely because of the production of poor seed. A few seedlings have been observed on the gravelly foothills of the Jornada range, but none were charted on the quadrats in this special study. Jackson ('28) found that the 1926 collections of *B. eriopoda* seed on the Jornada range were simply sterile florets, and obtained no germination in any of the samples. Wilson ('31) obtained germination percentages as high as 11.5 per cent from samples collected above 4400 feet elevation but the average germination for all samples of *B. eriopoda* seed collected from 1923 to 1929 was only 3.72 per cent.

Since it reproduces almost entirely by vegetative means, its restoration on depleted areas is necessarily slow, especially where it has been eliminated. Study of the plant has shown that cattle will eat it to within a half inch of the ground if feed is scarce, but that such close use is fatal if continued. At least two inches of stubble and 15 per cent of the flower stalks must be left on the ground each year, if a reasonably good stand of *B. eriopoda* is to be maintained.

Gutierrezia sarothrae

This is a woody perennial of the Asteraceae, from 6 to 36 inches high, with numerous erect stems growing from a woody base. The leaves are linear, and the heads are small and numerous on the paniculate inflorescences at the summits of the stems. Observations have shown that viable seed are matured in sufficient numbers to produce numerous seedlings on the range in favorable years. The seedling establishes a deep taproot during the first season, and develops abundant lateral roots as it matures (fig. 3). Campbell ('29) observed that the development of lateral roots is more conspicuous when the plant is isolated than when it grows near other plants. Branches of the more mature specimens often produce adventitious roots when they are partially covered with drift sand.

In contrast to the high forage value of *B. eriopoda,* the *Gutierrezia* seldom is eaten by cattle on the Jornada range. Dayton ('31) reports that it is reputed to be fair browse for cattle and horses, during the spring and fall in Utah and eastern Nevada, presumably because there is no better feed available. It is regarded by many stockmen as poisonous to livestock if eaten in considerable amounts. Rodents cut off many branches of the plant, and jack rabbits, *Lepus californicus texianus,* often rest in the shade of the larger bushes. As pointed out by Jardine and Forsling ('22), its presence in dense stands on the range may be taken as an indication of over-grazing, but Campbell ('29) has shown that it aids greatly in stabilizing loose windblown soils in the *Prosopis* sand dunes.

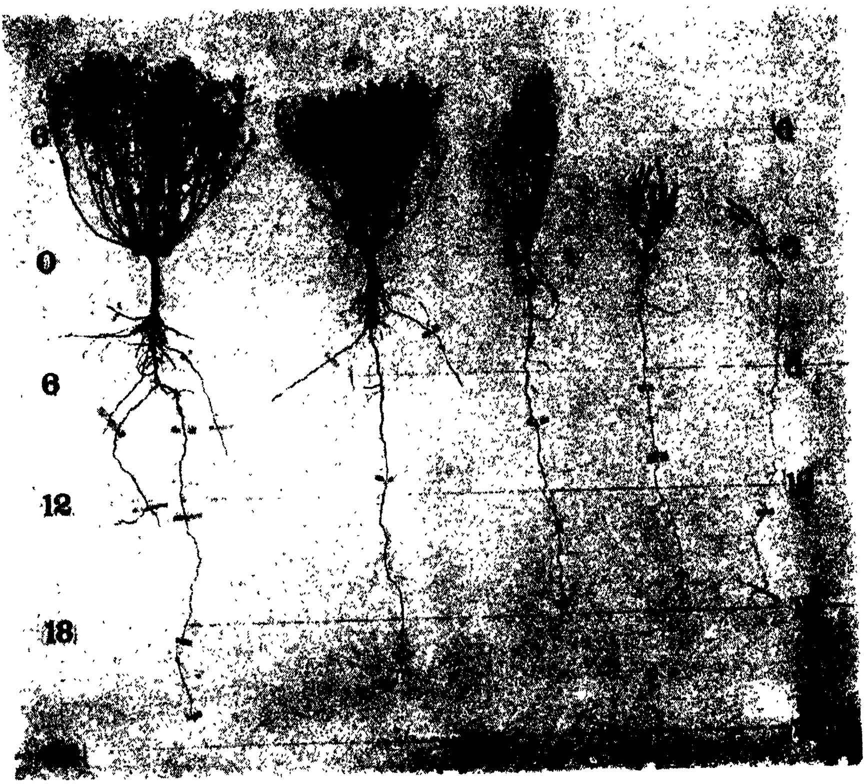

FIG. 3. *Gutierrezia sarothrae*, showing stages of development from seedling to mature plant. Dimensions in inches.

RESULTS OF QUADRAT STUDIES

Prior to the establishment of the quadrats, the area in which they were located had been fully utilized nearly every year from 1915 to 1924. In 1917, 1920 and 1921, the area was overutilized slighty. In addition, six of the ten years were well below average in summer rainfall, three were approximately average, and only one was well above average. Although the area was conservatively utilized in 1924, when the quadrats were established, the summer rainfall was only 1.82 inches, or about one-third of the average summer rainfall for the area.

As a result of these conditions, only 10 per cent of the soil surface was covered with vegetation in 1924. The plant cover was 63 per cent *B. eriopoda*, 20 per cent *G. sarothrae* and 17 per cent other plants. Thus the area was in a depleted condition with enough soil space available for both the grass and the shrub to spread during the more favorable climatic conditions and light utilization which prevailed from 1925 to 1930.

Table I shows the numbers of specimens and tuft areas at one inch above the ground of *B. eriopoda* and *G. sarothrae* on Quadrat 1, in the fall of each year from 1924 to 1930, with summer and total annual rainfall at a station 1.25 miles northwest of the quadrats, and grazing use of the study area from 1923 to 1930.

TABLE I. *Tuft numbers and areas of Bouteloua eriopoda and Gutierrezia sarothrae, precipitation and grazing use on Quadrat 1, 1923 to 1930 inclusive*

Year	Precipitation Annual	Precipitation Summer seasonal	Grazing use	Bouteloua Tuft area	Bouteloua Tufts	Gutierrezia Tuft area	Gutierrezia Plants
	Inches	*Inches*	*Per cent*	*Sq. cm.*	*Number*	*Sq. cm.*	*Number*
1923	8.79	3.53	100	—	—	—	—
1924	3.57	1.82	85	836	158	219	13
1925	7.06	4.01	0	851	117	67	5
1926	18.53	8.95	0	677	133	208	7
1927	9.30	8.31	0	1854	115	730	6
1928	9.52	3.68	25	1958	136	522	5
1929	13.80	8.94	15	4092	155	646	21
1930	6.77	4.61	15	4061	157	405	4

In considering table I, it is essential to remember that the summer growing season began usually in early July and ended in October, when the quadrat, three square meters in area, was mapped. The utilization estimates are so calculated that 100 per cent represents proper use for the type.

When Quadrat I was first mapped, the small *Gutierrezia* plants apparently were well established, but the *Bouteloua* was dominant, and both species were rather low in area. During 1924 and 1925, the *Gutierrezia* plants were attacked by beetle larvae, *Crossidius* sp.,[4] which establishes galleries in the woody roots and lower stems of the plants. As a result of this infestation, and the extremely low rainfall in 1924, 8 of the shrubs died in 1925. These conditions had a delayed effect upon the *Bouteloua,* as is shown by its reduced tuft area in 1926. Its subsequent steady gain resulted from the exceptionally high rainfall from 1926 to 1929, with only the summer rainfall of 1928 falling below average. The exclusion of livestock from the area from 1925 to 1928, and the light utilization during the remaining years, also facilitated the spread of the grass tufts.

While the *Bouteloua* was increasing steadily in tuft area, the *Gutierrezia* was attacked by leaf rollers in 1927, so that two shrubs had died by 1928. As a result of the high spring and summer rainfall in 1929, 16 *Gutierrezia* seedlings started that year, but during the dry winter and spring of 1930, all of these seedlings and one older shrub died. In 1930, the 4 surviving shrubs occupied nearly double the quadrat area of the 13 original plants. They were in fairly good condition, with an average height of 28 cm. and an average extreme diameter of 24 cm. It is important to note that none of the 18

[4] Adult beetles collected on flowers of *G. sarothrae* in 1932 were determined as *Crossidius pulchellus* Lec., by Dr. O. Park, Dept. of Zoology, University of Illinois.

seedlings which appeared during the 6 years survived, and only 30.7 per cent of the original *Gutierrezia* plants were left in 1930.

Table I shows that the changes in the *Bouteloua* tuft area, and in *Gutierrezia* numbers and tuft areas, may be correlated fairly readily with climatic and biotic influences. The numbers of *Bouteloua* tufts are more difficult to correlate because they vary as a result of the following possible reactions: (1) reproduction by stolons and rooting sets, (2) the consolidation of several small tufts during years favorable for growth, (3) the disintegration of large tufts as a result of unfavorable growth conditions, and (4) the death of tufts.

The rainfall and utilization data in table I apply also to table II, which shows the tuft numbers and areas for the *Bouteloua* and *Gutierrezia* plants on

TABLE II. *Tuft numbers and areas of Bouteloua eriopoda and Gutierrezia sarothrae on Quadrats 2 and 3*

	Quadrat 2				Quadrat 3			
	Bouteloua		Gutierrezia		Bouteloua		Gutierrezia	
Year	Tuft area	Tufts	Tuft area	Plants	Tuft area	Tufts	Tuft area	Plants
	Sq. cm.	*Number*	*Sq. cm.*	*Number*	*Sq. cm.*	*Number*	*Sq. cm.*	*Number*
1924	706	138	190	8	386	81	608	37
1925	562	106	62	5	473	62	69	7
1926	1066	96	284	7	653	57	320	28
1927	1773	96	524	8	1428	81	628	23
1928	1767	121	427	8	1901	110	536	23
1929	3768	144	596	8	3611	120	908	24
1930	3900	134	591	7	3107	114	751	21

Quadrats 2 and 3 from 1924 to 1930. These quadrats show much the same general trend as Quadrat 1, but since they were established under somewhat different conditions, they require individual analysis.

When Quadrat 2 was established, *B. eriopoda* was decidedly dominant, and only 8 *Gutierrezia* seedlings were present. During the six years of study, the changes in *Bouteloua* tuft area practically paralleled those on Quadrat 1; except that the drop in area as a result of the dry conditions during 1924 came in 1925, instead of in 1926 as on Quadrat 1. In addition, the *Bouteloua* area continued to increase on Quadrat 2 in 1930.

A severe mortality of *Gutierrezia* seedlings occurred on Quadrat 2 in 1925, and new seedlings appeared the two following years, just as on Quadrat 1. Of four seedlings which appeared on Quadrat 2 during the six years, only one survived, while 5 of the original 8 *G. sarothrae* plants lived through the period; and one plant, outside the quadrat at first, grew so large that it was charted on the area after 1926. In 1930, all 7 plants were in fairly good condition, with an average height of 21.5 cm., and an average extreme diameter of 30.3 cm.

Table II shows also the data for Quadrat 3, which in 1924, supported only 386 sq. cm. of *Bouteloua* and clearly was dominated by the *Gutierrezia,* mostly large mature plants, with a total quadrat area of 608 sq. cm. On this

plot the *Bouteloua* tuft area increased steadily to a maximum of 3611 sq. cm. in 1929, but suffered a small loss in 1930.

The most serious *Gutierrezia* mortality of all three plots occurred on Quadrat 3 in 1925 when 30 plants died, but 19 seedlings started in 1926, and two other plants, originally outside the plot, grew enough to be mapped on the quadrat. During the remainder of the study, 12 plants died, but 5 seedlings came up. Of the 24 seedlings which started on the quadrat in six years, 16 survived; and of the plants on the quadrat when it was established, all of the mature specimens died, and only three of the younger plants survived, while two outside plants grew onto the quadrat. In 1930, the average height of the surviving plants was 21.0 cm., with an average extreme diameter of 20.0 cm.

A recapitulation of the quadrat data shows that both *B. eriopoda* and *G. sarothrae* may be found in a depleted condition as a result of continuous drought, that both may recover during years with above average rainfall, especially the *Bouteloua* when it is utilized lightly. It appears that the large mature plants of *G. sarothrae* are quite susceptible to insect injury, as was shown by Quadrat 3 in 1925; that the well established seedlings from 2 to 4 years old are more resistant to both insect and drought conditions; and that one year seedlings are very susceptible to death during periods of low rainfall, as shown by the high mortality on Quadrat 1 in 1930. It appears further that if *B. eriopoda* is too seriously depleted, as on Quadrat 3 in 1924, the *Gutierrezia* becomes so well established that it covers more area for many years after the depletion than it does on areas where the *Bouteloua* was not so badly depleted, as on Quadrats 1 and 2. It is interesting to note that the maximum combined quadrat area of the *Bouteloua* and the *Gutierrezia* was very close on all three quadrats, 4738 sq. cm. on Quadrat 1 in 1929; 4491 on Quadrat 2 in 1930; and 4519 on Quadrat 3 in 1929.

No conclusive evidence was obtained as to the results of direct competition between the two plants, but in 1927, examination of 50 tufts of the grass growing very near or just under the crowns of mature *Gutierrezia* plants showed a repressing effect on the *Bouteloua*. In many instances the leaves and shorter flower stalks of the grass were wilted or dead; and many tufts showed a retardation of from one to two weeks in the flowering period. In spite of these retarding effects, very few dead *B. eriopoda* plants were found, and on most tufts at least one or two flower stalks grew clear of the *Gutierrezia* plant and developed a spike. Some of the stalks grew vertically and flowered above the bush, but most of them grew horizontally on the soil until clear of the *Gutierrezia,* then turned upward and flowered.

Vegetative Changes on the Experimental Area as a Whole

Table III shows the estimated proportion of soil surface covered by *B. eriopoda, G. sarothrae,* and other classes of vegetation, and the total vegetative cover of the association in which the quadrats were located, for each year

from 1924 to 1930. These data show that in 1924, only 10 per cent of the soil surface was covered with vegetation, estimated on a vertical projection downward of all plant cover. In general these ocular estimates correlate very well with the quadrat data; except for 1925, when an increase in the *Gutierrezia* was recorded, while the quadrats showed a marked reduction. By 1930, substantial increases in area for both the *Bouteloua* and the *Gutierrezia* were shown in both records.

TABLE III. *Estimated proportions of soil surface covered by vegetation on the experimental area, 1924 to 1930 inclusive*

Year	*Bouteloua eriopoda*	Other perennial grasses	Forbs and annual grasses	*Gutierrezia sarothrae*	Other shrubs	Total vegetation
	Per cent	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*
1924	6.30	0.65	0.80	2.00	0.25	10
1925	8.00	4.00	4.80	2.80	0.40	20
1926	12.90	3.30	10.50	2.70	0.60	30
1927	24.00	3.60	8.00	3.20	1.20	40
1928	24.15	3.15	3.50	3.15	1.05	35
1929	24.45	3.15	1.40	4.90	1.10	35
1930	26.60	1.75	1.45	4.20	1.00	35

The behavior of perennial grasses other than *B. eriopoda,* principally *Sporobolus flexuosus, Aristida pansa* and *A. purpurea,* is significant, as it places them in an earlier stage of succession than the *Bouteloua,* a fact previously inferred in a study of plant succession in *Prosopis* sand dunes (Campbell, '29). These three large, coarse-rooted grasses, all of which reseed rather readily, spread from 0.65 to 4.00 per cent ground cover during 1925, the first year following the severe summer drought of 1924; while the *Bouteloua* increased only slightly, and the *Gutierrezia* suffered from the infestation of *Crossidius* larvae. As the *Bouteloua* and *Gutierrezia* gradually spread after 1925, the three pioneer grasses were reduced in cover percentage. The highly ephemeral value of forbs and annual grasses, also pioneers, is shown by the decided variation in percentage of cover they furnished.

It is evident from table III that the grazing capacity of the study area increased steadily throughout the period of the experiment, along with the consistent spread of *B. eriopoda* each year. The outstanding feature is that the *B. eriopoda* covered approximately 4 times more surface from 1927 to 1930 than in 1924, in spite of the comparatively large proportion of *G. sarothrae* present. It is probable that the grazing capacity of the area would have been even greater, had the *Gutierrezia* been replaced by *B. eriopoda;* but even as the association existed in 1930, it was one of the highest grazing capacity ranges in southern New Mexico.

MANAGEMENT OF BOUTELOUA ERIOPODA RANGES

Even after serious depletion of the *Bouteloua eriopoda* by drought and overutilization, the natural trend is for the restoration of this valuable forage

species during favorable growth years if it is conservatively grazed. The disastrous results of interfering too greatly with this trend may be observed on almost any uncontrolled range in the southwest, where palatable plants have been so seriously depleted by overutilization year after year, that the unpalatable plants such as *Gutierrezia sarothrae* and similar species are now dominant.

The features of range management which are essential to facilitate the natural upward trend of forage production on the *Bouteloua* ranges have been shown by other studies on the Jornada range (Campbell, '31). They include (1) accurate determination of the grazing capacity of each range unit, with the extent of variation due to drought, (2) the actual stocking of the range on a conservative basis during the fall-winter and spring seasons, to allow the fullest vegetative reproduction and forage development of *Bouteloua eriopoda* during the summer grazing season, and (3) an accurate check on vegetative conditions by means of quantitative measurements.

Summary and Conclusions

Bouteloua eriopoda, the most important forage grass in southern New Mexico, and of considerable value as range forage throughout the semi-arid southwest, is subject to serious depletion as a result of drought or overgrazing or both. Its revegetation ordinarily is quite slow because it reproduces poorly by seed, and migrates almost entirely by vegetative processes.

Gutierrezia sarothrae has been observed to replace the *Bouteloua* on areas continually overgrazed. This dominance of the worthless shrubs is due largely to the fact that usually they are not relished by range livestock under ordinary conditions, while the palatable forage grasses may be killed entirely by injudicious grazing, especially during drought. Nevertheless, these shrubs have a definite soil protective value. A study of the occurrence of *G. sarothrae* in a representative *B. eriopoda* association on gravelly sand was started in 1924. The area had been badly depleted by severe drought and some overgrazing. Three quadrats, each containing three square meters were established and charted every year from 1924 to 1930 inclusive.

On the first quadrat, several well established young *G. sarothrae* plants were present in 1924, but *B. eriopoda* was dominant. In spite of attacks by insects in 1925 and 1927 nearly 31 per cent of these plants were alive in 1930, but no new seedlings survived, although many appeared. As a final result of generally above average rainfall and light grazing, the *Bouteloua* area was nearly 5 times greater and the *Gutierrezia* area nearly two times greater in 1930 than in 1924.

On the second quadrat, the *Bouteloua* was decidedly dominant in 1924, and only a few seedlings of *Gutierrezia* were present. 62.5 per cent of the young shrubs survived, while only one new seedling of four became established. By 1930, the *Bouteloua* tuft area was nearly 6.5 times greater, and the *Gutierrezia* area over 3 times greater than in 1924.

The last quadrat supported some *B. eriopoda,* but large mature *Gutierrezia* plants were dominant in 1924. The drought and beetle larvae damage caused so great a mortality among these mature plants that none survived and only three young plants existing in 1924 lived through to 1930. However, on this quadrat, nearly 70 per cent of the seedlings survived, largely as a result of fortunate rainfall distribution during their early growth in 1926 and 1927.

The quadrat data and ocular estimates of composition for the association in which the quadrats were located, show that both *Bouteloua eriopoda* and *Gutierrezia sarothrae* may be depleted as a result of severe drought, such as occurred in 1924. Both species may recover during years with above average rainfall, especially the *Bouteloua* if it is grazed conservatively after it has matured. Although the *Gutierrezia* has a high mortality rate, individual specimens grow to a size sufficient to be prominent even in the climax *B. eriopoda* association.

Observations made on the experimental area show that from 1927 to 1930, its grazing capacity was approximately 4 times greater than in 1924, in spite of the relatively large proportion of ground covered by the *Gutierrezia* during the entire period of study.

All species in the association may be injured by drought, but the trend is toward a decided increase in grazing capacity during years with higher rainfall. Careful range management that encourages this trend will assure sustained range forage production. Injudicious grazing may so deplete the palatable grasses that the shrubs dominate, the soil loses its stability, and grazing values become so low as to require decades for their restoration.

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REVIEWS

Conation and Perception in Animal Learning [1]

Since Thorndike's classical experiments, carried out in the closing years of the last century, a voluminous literature has grown up around the subject of animal learning. It seems unfortunate to Russell that so much valuable research on this important subject is reported only in psychological publications where it is seldom seen by biologists. He deplores the state of isolation which so generally seems to prevail between these related sciences and hopes that this review will help to acquaint zoologists with psychological research in this field.

Starting with the chronologically appropriate subject of Thorndike's theory of learning, he discusses the experimental evidence upon which these laws were based. He then proceeds to consider the numerous criticisms which have been launched against these views, criticisms which were first made by Mills in 1898–99 and which have continued to the present day.

The phase of the subject next receiving attention is that of Connectionism or the connection between situation and response. Thorndike concluded that this connection was neural in nature and that the individual neurones inherit avoiding reactions from their protozoan ancestors, that in other words "the learning of an animal is an instinct of the neurones." The outstanding researches of Lashley are called upon as evidence against this older theory which considers learning to be a 'wearing-smooth' of pathways. It is recalled that Lashley has found deterioration of maze-learning capacity to be roughly proportional to the amount of cortical injury rather than to the position of that injury; also that disturbances in previously learned maze-reactions due to later operation by thermocautery show that this disturbance is roughly proportional to the extent of the cortical injury.

In the remaining main section of the paper the literature on conational and perceptual factors is reviewed. Conation is defined as "an attempt on the part of the organism to change its state, in relation to environment, in such a way that an end or goal is achieved and the activity ceases." It is a study of the change from ill-adapted or random activity to well-directed conative activity involving a change in the perceptual situation.

The difficult subject of gestalt psychology is considered under the same main heading. The fundamental assumption of this school is that an organism reacts to an actual constellation of stimuli by a total process rather than to a multitude of individual and independent stimuli. An interesting experiment carried out by Bierens de Haan is given as an illustration of this "Prin-

[1] **Russell, E. S.** 1932. *Biological Review* 7: 149–179.

ciple of the Whole" as the gestalt school is sometimes described. Using the cuttlefish *Octopus vulgaris,* Baerens de Haan showed that a crab creeping along the bottom would be attacked and devoured whereas a crab suspended from above would provoke only an attempt at removal by means of a stream of water on the part of the cuttlefish. The implication here would be that the cuttlefish had been accustomed to react to a total situation involving a crab crawling along the sea bottom. A crab suspended from above brought about a new and heretofore unfamiliar configuration in which the crab was not perceived as such. Lastly the theories of Tolman are considered, theories which are based on the gestalt principle.

Considering the paper as a whole, Russell has made a very excellent attempt at summing up a vast and divergent literature upon a subject which Lashley considers to be in a state of confusion. As a result of this condensation many theories appear absurd or unreasonable which would doubtless be more convincing if dealt with at greater length by their respective authors. The review should prove a valuable reference-source for biologists interested in the psychological interpretation of animal learning.

D. C. G. MacKay

University of Chicago

Ecology of Jackrabbits[1]

This publication exhibits the physical form of a technical bulletin but carries the mental atmosphere of an ecological monograph. Barring such books as Stoddard's "Bobwhite" and Friedman's "Cowbirds," few recent works have described a single species (or, in this case, a pair of species) from so many and such diverse angles.

The Biological Survey's "Outline for Mammalian Life Histories" evidently furnishes the framework for the text, but the writers have somehow clothed its dry bones with living tissue. Few pages will escape the reader's pencil, checking some noteworthy new viewpoint or new fact. The treatment is quantitative in a sense quite beyond the usual weighing of stomach contents. Ratios, indices, densities, and frequencies, as well as averages, abound. One has the impression that enough mental tools have been assembled to build a much larger structure, which will, I hope, be forthcoming.

It is fitting that such a work should end with no 'conclusion' to settle the moot problems of rabbit and predator control. Poisoning is granted no absolution. Neither is there any dogma of letting nature alone. Control is viewed as a local problem. "Man can never destroy the balance (of nature), any more than he can prevent the conservation of energy. The new balance may be more to his liking, or it may be extremely harmful to him. It is man's job to understand the balance well enough to be sure, when he changes it, that the new . . . will be to his advantage." While the authors repeatedly assert

[1] **Vorhies, C. T., and W. P. Taylor.** 1933. The life history and ecology of jack rabbits in relation to grazing in Arizona. *Univ. Arizona Tech. Bull. No. 49, Tucson.*

that their viewpoint but mirrors the Biological Survey's official policy, one cannot suppress the thought that it unduly flatters its actual field practice.

One gathers a clearer picture of Arizona, as well as of jackrabbits, from this work. Particularly impressive is the evidence of a neo-tropical ecology as indicated by yearlong breeding and the absence of cycles. The authors have likewise augmented the growing array of evidence that overgrazing by livestock lies at the root of most of the ecological retrogressions so far suffered by the biota of this teeming 'desert.'

No student could approach a subject from so many angles without some exhibiting weakness: in this case it seems to me the section on parasites and diseases. As in the case of many older investigations, the emphasis is on gross pathology, with no avowed realization that bacterial and virus diseases may play a coordinate or even greater rôle, a probability which should not go unacknowledged because it remains unexplored. The biological Survey's own work on the bacterial diseases of rabbits (Green), is not cited. This 'blind spot' may likewise explain the (to me) uncalled-for disparagement (on p. 555) of the findings of the Matamek Conference on disease cycles.

Be this as it may, Vorhies and Taylor have made a large and welcome contribution to desert ecology, and have laid one more foundation stone for southwestern conservation.

Aldo Leopold

University of Wisconsin

Backgrounds of Biota [1]

In dealing with distribution and succession of major faunas and floras, as well as in tracing the development of environments and habitats, the ecologist must use geological data. For some of these, he may consult sources; for many (and especially, for viewpoints and syntheses) he must use summaries which are, or approximate, textbooks.

Schuchert and Dunbar provide much information of a thoroughly modern nature. Organizing even historical chapters about principles, they both trace the evolution of the earth's surface and stress the underlying factors. They treat relief, climates and drainage systems. By good illustrations, many of which are new, they link both life forms and faunas with changing conditions. Plants receive less attention, but for them an adequate review may be found in Seward's "Plant Life through the Ages." Ecologists in doubt about geologists' methods will find these well developed.

[1] **Schuchert, Charles, and Carl O. Dunbar.** 1933. Textbook of Geology, part II. Historical Geology, 3d edition. Pp. vii + 551, 332 figs. *John Wiley and Sons, New York.* $4.00.

Moore, Raymond C. 1933. Historical Geology. Pp. xiii + 673, 413 figs. *McGraw-Hill Book Company, New York.* $4.00.

Field, Richard M. 1933. The Principles of Historical Geology from the Regional Point of View. Pp. xii + 283, 108 figs. *Princeton University Press, Princeton.* $3.50.

Moore provides abundant data but fewer syntheses in a book which holds closely to standards set by Chamberlin and Salisbury in their three-volume "Geology," a work unfortunately now out of data, and of doubtful value for ecologic reference. Those interested in the development of western North America will find Moore's volume of special value. In reviewing Fenneman's "Physiography of the Western United States" I stressed its value in ecologic or zoogeographic studies of the West, and biologic travel through the regions treated. Moore carries this treatment into the past, with a bibliography of the most significant papers. Though less useful than the volume by Schuchert and Dunbar, it will save much searching for sources.

Dr. Field's chief concern is to develop a new method of teaching historical geology. In so doing, he develops the principles of stratigraphy and correlation, principles on which ecologists often rely without very clear understanding. He also traces the geologic development of typical regions such as the Grand Canyon of the Colorado, Yellowstone National Park and the Appalachians, showing clearly the relationships of past development to present biota. The book deserves better illustrations. For these one must consult sources, or the ever-useful Schuchert and Dunbar.

C. L. Fenton

West Liberty, Iowa

Forestry

The silvicultural aspect of forestry being one of the phases of applied ecology, all ecologists should be interested in the recent statement of the forestry problem by Pack.[1] He appreciates the fact that in common with all ecological problems, the forestry situation is complicated in the extreme. This complication is made the more complex from its dependence upon economics with their fluctuations and changes.

The changing requirements of our population have changed their demands upon forest products. These changes are presented and prove the need of re-thinking the whole forest situation. Emphasis is put upon the fact that forestry must be based on sound economic considerations rather than upon idealistic theories.

The chapter headings of the book are: Re-thinking forestry; From crusade to economic problem; Forest use; Private enterprise; Public forest administration; Foresters and forest education; and Regional planning and economic policy. These give a good idea of the topics discussed. The discussion seems to be critical, fair, unprejudiced, and presented in a form that will interest both the ecologist and the economist.

Geo. D. Fuller

The University of Chicago

[1] **Pack, Arthur Newton.** 1933. Forestry: An economic challenge. Pp. iv + 161. *Macmillan Company, New York.* $1.25.

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NOTES AND COMMENT

Is There a Natural Crop Rotation in Forests?

The establishment in forests of reproduction other than that of the present dominants is usually interpreted as evidence of succession. Usually the site becomes occupied by progressively more mesophytic species, or those more tolerant of shade and competition, and able to become established on deeper accumulations of litter. In forests under management the natural course of succession is rarely allowed to proceed far, but is repeatedly thrown back to the earlier sere due to lumbering.

Foresters have long observed these common phenomena, and indeed all methods of natural reproduction are predicated on either maintaining the existing sere (as in tolerant selection forests) or throwing back succession to a point where the desired crop species will find optimal seedbed conditions. It is also common observation that not only is this irreversible successional tendency present in forest reproduction, but that habitat conditions under individual trees often appear inimical to the reproduction of the same species. In some cases the reproduction which occurs exhibits a tendency contrary to natural succession. Apart from studies of toxic substances excreted by roots, such as *juglone* in the case of black walnut, there have been few careful investigations; but a considerable body of general observations have convinced many foresters that there is a natural "crop rotation" in forests, superimposed on the succession of the community as a whole.

In a recent paper under the title "the requirement of forest soil for crop rotation" Wallmo [1] presents additional evidence in support of the hypothesis that a tree will not reproduce in its own litter as well as under another species. In earlier papers [2, 3] examples were cited from observations made in the spruce-fir forests of the Vosges and Jura since 1890, as well as in Switzerland. Wallmo now gives numerous examples from Austria and Sweden. In irregularly-cut peasant forests in Austria scotch pine, *Pinus silvestris* L., was observed reproducing under pure spruce stands to the virtual exclusion of Norway spruce, *Picea excelsa* Link, and on sites where the shade was believed too dense for pine. Pine seedlings appeared more vigorous than spruce. Similar illustrations are given from Sweden. The establishment of spruce under pine is of course much more common in all parts of the world. But cases of even birch coming in under conifers as cited by Wallmo seem "unnatural" rather than the opposite. A careful study of the vegetation and physical factors in such cases would probably show that some external influence has initiated a new sere. Unfortunately Wallmo presents no such data.

Jensen [4] has cited similar examples of succession on Danish heaths, and the failure of successive generations of *Sorbus* and other trees of the same family in the same nursery bed. Change of timber crops in the forest is frequently advisable due to infection of the soil with root rots such as *Fomes annosus*, or because of soil deterioration.

The writer in common with many American students of reproduction in spruce-fir forests of northeastern North America has frequently observed that balsam fir, *Abies balsamea* L., appears very abundantly under red spruce, *Picea rubra* Link, stands, while spruce seedlings may be practically wanting. Spruce appears to be more persistent under a closed canopy, however, and especially in competition with hardwoods. From studies made in northwestern Maine since 1924 the mortality of fir saplings has been far greater

[1] **Wallmo, U.** 1933. Skogsmarkens fordran på växelbruk. *Skogen* **20**: 133–137.
[2] **Wallmo, U.** 1929. Litet om blädning. *Skogen* **16**: 27–40.
[3] **Wallmo, U.** 1930. Produktionskrafterna i skogen. *Skogen* **17**: 322–335.
[4] **Jensen, C. F.** 1931. Generationsveksel i skoven. *Skogen* **18**: 52–54.

than that of spruce. Many such cases of apparent alternation of species may be explained by relative differences in the efficiency of seed production (production less losses) of the different species concerned. Surprisingly little is still definitely known of the specific differences in seedbed requirements of associated species. Until carefully controlled experiments have proven otherwise it would seem best to explain all cases of crop rotation by the natural laws of succession operating in each forest association.

HENRY I. BALDWIN

PENN STATE FOREST SCHOOL,
STATE COLLEGE, PA.

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CERTAIN CONDITIONS OF EXISTENCE OF FISHES, ESPECIALLY AS CONCERNS THEIR INTERNAL ENVIRONMENT[1]

EDWIN B. POWERS

University of Tennessee

Throughout the period of accurate observations, much work has been done on living organisms with an attempt to determine the conditions of their existence. At the present time this is occupying the minds of a number of investigators in both the botanical and zoological fields.

During this year the Ecological Society of America will have held two symposia: one, at the Chicago summer meeting, on the conditions of existence of aquatic animals and the other on oceanography here at Boston.

In these symposia nutrition, and especially the source of nutrition, has been stressed. The physical and chemical factors affecting living organisms and the response of certain organisms have also been considered. In all, the animals have received most of the consideration.

There are certain newly discovered facts bearing upon the conditions of existence of fishes that I would like to discuss briefly this evening. I am well aware that we have a mixed audience. There are many botanists present. But I hasten to state that a cobbler should stick to his last. Thus, I have chosen as my subject, *certain conditions of existence of fishes.*

When we consider the conditions of existence we think of two environments, an external and an internal. Winton and Bayliss, in the opening chapter on *The Blood and Other Body Fluids* in their " Human Physiology " ('31), state: " The continuous circulation of the blood keeps the fluid surrounding the tissue cells—the ' internal environment '—sensibly uniform in composition throughout the animal. The blood, however, plays a far greater part than that of an indifferent circulating fluid; and its properties are such that, in itself, it has a very important action in stabilizing the composition of the internal environment towards the disturbing influences of activity or of alterations in the external environment." Physiologists accept a statement such as

[1] Presidential address before the Ecological Society of America at the Boston meeting, December 28, 1933.

the one just mentioned as comparable to an axiom, when it is applied, at least, to the higher mammals.

I will further restrict my remarks to the internal environment of fishes; that is, the physiology and the physico-chemistry of the blood. The knowledge of the blood as a chemical system of the higher forms is approximately complete (Y. Henderson, '25).

When one factor of the system changes it calls forth predictable changes in all the other factors (L. J. Henderson, Bock, Field and Stoddard, '24).

It is the physiology of the blood as a medium of respiratory exchange that we wish to consider. We will gather the scattered bits of knowledge and see if we cannot make of it a whole that is at least a patch-work quilt.

As early as 1919, Krogh and Leitch called attention to the fact that the loss in affinity of fish blood for oxygen was very marked with rise in carbon dioxide tension. This factor was further exemplified in a paper read by the present author in 1929 before the annual meeting of the Ecological Society of America and published in 1932 (Powers and Hickman). Root ('31) showed that this characteristic was quite marked. Drawn blood of a sea robin loses as high as 70 ± per cent of the original affinity for oxygen when exposed to a carbon dioxide partial pressure of approximately 3.1 per cent of an atmosphere. This is approximately 103 times the normal [2] for fish blood, *i.e.*, 103 times the carbon dioxide partial pressure of the air. Is this a physico-chemical characteristic peculiar to fish blood, or is it in common with mammalian blood? It had already been shown (Barcroft and Means, '13; Barcroft '28) that this is also a characteristic of mammalian blood when exposed to an abnormally high carbon dioxide partial pressure. Rona and Ylppo ('16) found that the hemoglobin of mammalian blood had the least affinity for oxygen at its iso-electric point and that its affinity for oxygen increases both with an increase and decrease in the hydrogen ion concentration from this point. The iso-electric point of the hemoglobin of drawn blood of the yellow cat, *Leptops olivaris* (Rafinesque), was found experimentally to correspond to a carbon dioxide tension of 0.344 per cent of an atmosphere (Powers and Hickman, '32) (table I and fig. 1). When fig. 1 is examined further it is found that the blood of the yellow cat continues to gain in affinity for oxygen with increase in carbon dioxide tension until about 1.4 per cent of an atmosphere is reached. From this it follows that a yellow cat could not extract oxygen from water having a carbon dioxide tension between approximately .344 per cent and approximately 1.4 per cent of an atmosphere. This, of course, is providing that blood in the circulatory system of the fish would not

[2] The blood in the gas-gland of a deep sea fish is normally exposed to higher carbon dioxide partial pressures (Schloesing and Richard, '96; Haldane, '98). This characteristic is of prime importance in the deposition of gases into the swim-bladder of fishes. There is no more direct application at the higher carbon dioxide tensions to the physiology of normal respiration of fishes than there is at the higher (above normal) carbon dioxide tensions of the blood of mammals in normal mammalian respiration.

TABLE I. *Data taken from table XIX, Powers and Hickman ('32). Data given show the oxygen contents of drawn blood of the yellow cat, Leptops olivaris (Rafinesque), when equilibrated with approximately 20 per cent oxygen to which different percentages of carbon dioxide had been added at 23°C.*

% of CO_2 in gas mixture equilibrated with	% of O_2 in gas mixture equilibrated with	Volume % of O_2 in blood
.015	20.00	12.75
.037	20.00	12.70
.078	20.00	12.67
.139	19.99	12.59
.239	19.97	12.39
.344	19.96	11.98
.444	19.96	11.99
.638	19.94	12.20
1.06	19.90	12.34
1.54	19.85	12.36
2.05	19.80	12.30
3.06	19.70	12.01

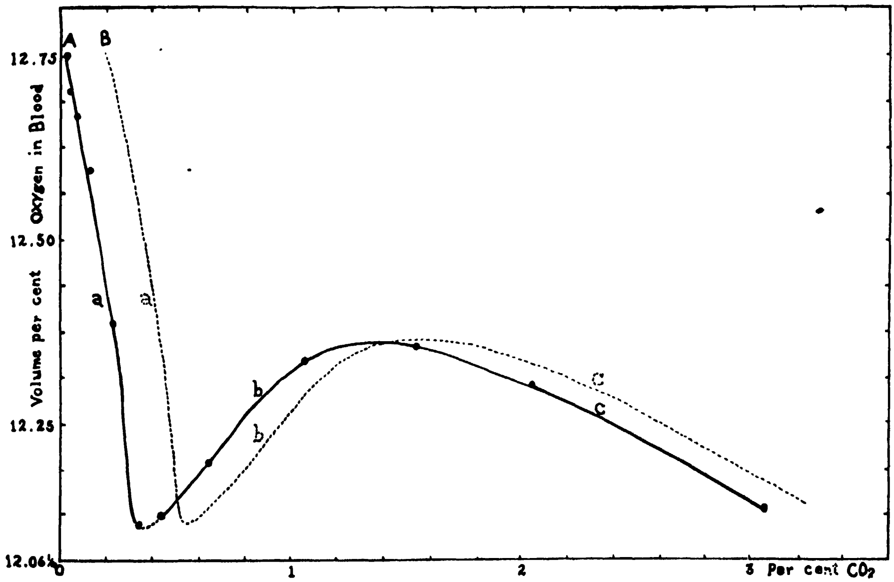

FIG. 1. Curve *A* is a graphic representation of data given in table I. Curve *B* is a hypothetical curve purported to represent a curve *A* of blood with a higher alkali reserve or carbon dioxide capacity and with a different red corpuscle count. *B* is drawn identical to *A* except in position, thus hypothetical.

increase its buffering capacity with increase in carbon dioxide tension to any greater degree than did drawn blood.

The fish blood does increase its buffering capacity or alkali reserve with an increase in carbon dioxide tension of the surrounding medium and *vice versa* (Powers, '22; Powers and Logan, '25; and Powers, Hopkins and Hickman, '32). The alkali reserve of fish blood is not only modified by car-

bon dioxide tension of the surrounding medium but is also affected by the oxygen tension of the surrounding medium. An increase in oxygen tension of the medium increases the alkali reserve of the blood and *vice versa,* at least as measured by the capacity of the blood to combine with carbon dioxide (Powers, Hopkins and Hickman, '32). The number of the red blood corpuscles is increased with a decrease in the oxygen content and by an increase in the carbon dioxide tension of the surrounding medium and *vice versa* (Hall, Gray and Lepkovsky, '26; Hall, '28; and Powers and Shipe, '32).

From this it follows quite obviously that a curve showing the affinity for or the capacity of fish blood to combine with oxygen when held in the circulatory system of the fish would be quite different from curve *A* or *B* shown in figure 1. Such a curve has never been investigated but information concerning its course would be quite helpful in increasing our knowledge of conditions of existence of fishes. The *a* portion, *i.e.*, up to the isoelectric point, of such a curve, at least in yellow cat fish blood, would be flatter. The flatness of this portion of the curve would depend upon the ability of the fish to increase or decrease the alkali reserve of its blood with variations of the carbon dioxide and oxygen tensions of the medium. The shapes of the *b* and *c* portions of the second curve cannot so easily be anticipated. By all means, the form of this second curve would not be as represented by the dotted line curve *B* of figure 1.

In light of curve *A* (fig. 1), what are the conditions of existence of fishes as to their respiration? Fishes would be able to extract oxygen from the water so long as they were working in the *a* range of the curve. They would not be able to do so in the *b* range. They would again be able to extract oxygen from water in the *c* range. The drawn blood in passing over the *a* range (fig. 1), has passed from a carbon dioxide tension of .015 per cent to .344 per cent of an atmosphere. From the equation $\mathrm{pH} = -ne - n\log P_{CO_2}$ (Powers, '30) the blood would have changed in reaction through a range of approximately 1.23 pH units depending upon how near *n* approximates unity. Starting with a carbon dioxide tension of .0344 per cent of an atmosphere, *i.e.*, approximately the carbon dioxide partial pressure of the air, the range would be 1 pH provided *n* equals one.

We are all aware that at least the higher mammals cannot tolerate a range of 1.23 or even 1 pH in their blood. The range of pH tolerance of blood among fishes has never been investigated. Fishes (Hall, '31) "have apparently no means by which gas tensions to which their gills are subjected may be altered." It follows that the fish must be able to modify the alkali reserve of its blood with changes in gaseous tensions of the medium. This factor has been investigated by the author and colleagues (Powers, '22; Powers and Logan, '25; Powers, Hopkins and Hickman, '32; and Powers and Shipe, '32). These investigations have been criticized by several workers. One worker went so far as to deny that the alkali reserve of the blood of a fish is modified with change in carbon dioxide tension of the surrounding medium. These

critics have been answered elsewhere and will not be further mentioned. Fishes do change the alkali reserve with changes in both carbon dioxide and oxygen tensions of the medium. The extent and rapidity of this change has not been determined. This should be determined for each species of fishes.

The explanation now becomes clear as to why a fish is able (Pruthi, '27) to extract oxygen from water in which a preceding fish had been asphyxiated. When the first fish died, if the carbon dioxide tension was within range *b*, a second fish with blood not yet modified placed in the same water would be in carbon dioxide tension range *c* and could extract oxygen. Or if a fish had been asphyxiated in water having a carbon dioxide tension of range *c* a second fish could still extract oxygen from the water. Both fish would die of acidosis and not because of "the direct influence of the hydrogen ions" as suggested by Pruthi ('27). The relation between the pH and aquatic animals has been summarized elsewhere (Powers, '30).

The problem for future investigation is not to determine whether or not fishes are able to alter their blood "in stabilizing the composition of the internal environment towards the disturbing influences of activity or of alterations in the external environment" but to determine the capacity of fishes to alter their blood to conform with an external environment, either dynamic or stable.

Fishes obviously could not continue to survive in water in which the carbon dioxide tension range is either *b* or *c*, since the hemoglobin would be on the acid side of its iso-electric point. In the case of the yellow cat the *a* range in drawn blood is passed when the carbon dioxide tension has reached approximately 0.34 per cent of an atmosphere. In the air this requires an addition of only approximately 3.1 ml. carbon dioxide to a liter. Approximately 55 ml. carbon dioxide has been added to the exhaled air of man under ordinary conditions. This is an increase of from .03 per cent of an atmosphere to 5.5 per cent.

When we think of a fish in terms of the physiology of respiration in mammals, it would seem that fishes would be more endangered by possible changes in the carbon dioxide tension of waters bathing their gills than mammals by modifications in the carbon dioxide partial pressure of the alveolar air. This is taking into consideration that 0.03 per cent is almost a vacuum and only a very small (0.3 per cent) increase in the carbon dioxide tension of the water is necessary to increase its original tension by ten. In spite of these facts and the additional fact that the respiratory organs of fishes are not well adapted to controlling the carbon dioxide tension of waters bathing their gills, the epidemic of the dying of fishes in natural waters and in rearing ponds (Pruthi, '32) sometimes observed are exceptions and not the rule. What is the real explanation? Distilled water at 0° C. and 760 mm. Hg pressure when in equilibrium with atmospheric air dissolves approximately 0.97 ml. of oxygen per 100 ml. of water. If a fish having a respiratory quotient of 0.80 should extract the whole of the oxygen in solution, it would give off .776 ml.

of CO_2 to the 100 ml. of water that bathed its gills. Because of the solubility of CO_2 (179.67 ml. carbon dioxide per 100 ml. water) in water this would raise the carbon dioxide tension of the water by only .43 per cent of an atmosphere. This is almost within the *a* range of the oxygen affinity curve *A* (fig. 1). We find here another adaptation of the environment (L. J. Henderson, '24). Water dissolves very little oxygen even when in equilibrium with the atmosphere. If all the oxygen dissolved in the water at 0° C. were changed to CO_2, the carbon dioxide tension of the water would be just sufficient to cause the (drawn) blood of the yellow cat to have passed on the acid side of the iso-electric point of its hemoglobin.

It now becomes clear why, after a series of cloudy days which prevent photosynthesis in rearing ponds in which anaerobic and ordinary oxidation are taking place and the carbon dioxide tension of the water has been raised to the *b* range of curve *A* (fig. 1), there will be an epidemic of dying fish. With the more sensitive fishes the *a* range will be very much restricted and the *b* range more often reached. Low oxygen aggravates the situation. Under such situations a fish must compensate by increasing the alkali reserve of its blood or be able to tolerate a wider range in pH of its blood than higher forms.

Pruthi ('32) gives the carbon dioxide tension as 3.31 mm. Hg and the oxygen content as 0.427 ml. oxygen per liter at the surface and 3.71 mm. Hg carbon dioxide tension and 0.16 ml. oxygen per liter at the bottom of a fresh water tank on a morning of severe mortality of fishes. The carbon dioxide tension given would be one hundred and more times as great as water in equilibrium with the air. Pruthi gave the pH of the water of low carbon dioxide tension as 8.6, 8.2, and 8.75 (average 8.52) and the high carbon dioxide tension water as 7.45 pH and 7.40 pH (average 7.425). When equation $pH = -nc - n\log P_{CO_2}$ is used in the calculation, it is found that the carbon dioxide tension will approximate .30 mm. Hg and not 3.31 to 3.71 mm. Hg. This, .30 mm. Hg, would be what one would expect unless there were ten times as much anaerobic oxidation taking place in the tank water as aerobic. The .30 mm. Hg carbon dioxide tension approximates the *b* range of the oxygen affinity curve of drawn blood of the yellow cat. Thus, the difficulty of sensitive fishes is quite obvious. The bringing about of the situation by a series of cloudy days during which photosynthesis was low and excessive oxidations in the water continued as suggested by Pruthi is perhaps correct.

When we consider the oxygen consumption of a fish, it is quite obvious that the oxygen necessary for the metabolic needs of the fish will be extracted from the water or the fish will suffer from oxygen want. If there is an oxygen debt it must be paid immediately or the fish must decrease its demand for oxygen. This can be done only by decreasing its metabolism. All know that there is no storage of oxygen. Experiments have been carried on (Powers, '23; Powers and Shipe, '28) which show that fishes are not so

well able to extract or utilize oxygen from the water immediately on changing the carbon dioxide of the water to a higher tension. The effect of changes in carbon dioxide tension is greater at lower oxygen contents of the water. These experiments were never intended to show the rate of metabolism of fishes in waters of different carbon dioxide tension, but they were intended to determine if there could be developed an oxygen debt.

Just at this point there has been reported a very interesting observation by Davidson ('33). Davidson reports the dying of the pink salmon by the hundreds "at sunset in a stream in southeastern Alaska." Trout and fresh-water bullheads suffered the same fate. The pH of the water where fishes were dying was 5.6. Just below in the same stream and below the falls, the pH was 6.1. Davidson's statement, "Had the acidity of the water in the stream where the fish were dying been due to a substance other than the presence of carbon dioxide, then the pH of the water below the falls would likewise have been 5.6," is doubtless a correct statement of facts.

Saunders' ('26) formula does not hold (Powers, '30). Harvey's ('28) findings that carbon dioxide tension increases in a non-linear manner with a decrease in the pH in water with low alkaline content is correct (Powers, '27; Powers and Bond, '27 and '28). This is also true of alkaline water (l. c.'s) and even blood plasma. But when the pH is plotted against the log of the carbon dioxide tensions ($pH = -nc - n\log P_{CO_2}$) the relation becomes linear. The fixed carbonate content was very low as shown by Davidson's titration figure and by the fact that the pH of the water was 6.1 when approximately in equilibrium with the carbon dioxide partial pressure of the air. As a matter of fact, "most of the water came from the melting snow in the mountains" and would approach in characteristics distilled water. From the slope of the linear portion of Byck's ('32) curve showing the relation between the logarithm of the carbon dioxide tension of distilled water and its pH and observation made in natural waters (Powers, '30) n in $pH = -nc - n\log P_{CO_2}$ for distilled water becomes .5000. From this point the value of n increases with increase in alkalinity and decreases with acidity of the water. Data given by Powers ('30 and citations) indicate that the value of n for the water of the stream described by Davidson ('33) approximates .6000. It follows that a drop of .4 in the pH of the water shows an increase of 100 per cent in the carbon dioxide tension of the water and not 50 per cent. This 100 per cent increase in the carbon dioxide tension of blood without increase in buffering capacity represents a difference of 0.30 pH ($pH = pK_1 + \log[BiK/CO_2]$). If 50 per cent increase with carbon dioxide tension of the water is taken as being correct there would be only 0.18 pH change in blood with a fixed buffering capacity. From this it follows that fishes are very sensitive to changes in the pH of their blood.

Davidson's suggestion that "It may be that the sudden change in the carbon dioxide pressure of the water in the stream . . . caused a drastic change in the respiratory function of the fish which resulted in the sudden

death of the salmon and other species of fish . . . ," is most likely correct. " . . . the opinion that the sudden stillness of the air (on August 6) formed a temporary blanket over the quiet stretch of water in the stream where the school of 80,000 salmon slowly milled about . . . caused a sudden rise in the carbon dioxide content of the water " is perhaps not the real reason for the sudden rise of the carbon dioxide tension of the water. The key to the situation is more than likely found in the facts that " The weather during the latter part of July . . . was cool and an abundance of rain kept the stream surging near the tops of its banks," " . . . the first week in August the weather changed and became fair and warm," there was " . . . a marked drop in the water level of the stream so that most of the water came from the melting snow in the mountains," and on August 5 and 6 " . . . the air temperature reached a maximum of 90° F." The rains must have been followed by a great deal of seepage water which is always steeped with carbon dioxide. On July 8, 1927, the author found water in a spring at Thatcher, Blakely Island, Puget Sound, formed mainly by seepage from a lake to have a carbon dioxide tension of approximately 0.4 per cent of an atmosphere. The sudden fall of temperature at sunset August 6 caused a fall in the relative amount of water from the melting of snow leaving a larger portion of the water to be derived from the high carbon dioxide tension seepage water. This change was sudden thus causing a sudden rise in the carbon dioxide tension of the water of the stream.

It now becomes plain that one very dangerous contamination of natural waters is carbon dioxide. An abnormal rise in carbon dioxide tension of the water can be brought about by contamination of alkaline water with an acid product which would cause liberation of carbon dioxide from the bicarbonates. If all the HCO_3 (average 116 parts per million, Birge and Juday, '11, p. 170) in Garvin lake were liberated as carbon dioxide, it would raise the carbon dioxide tension of the water by 3.24 per cent of an atmosphere, or it would increase the carbon dioxide tension of the water by over one hundred times the carbon dioxide partial pressure of the air. The carbon dioxide tension of Minoqua lake with 4.9 parts HCO_3 per million (least of HCO_3 contents of lake water given on p. 170, *l. c.*) would be increased by .134 per cent of an atmosphere under the same conditions. This would be 4.4 times greater than the carbon dioxide partial pressure of the air.

Effluents from tanneries are generally acid due to the presence of acetic acid. Any acid will liberate carbonic acid from bicarbonates in solution. Free carbon dioxide originates from carbonic acid.

Mr. Charles L. Clarke, a student in our laboratory, states that during the time a tannery was in operation at Walland on the Little River the turbines of the Peery mills about two miles below were stopped due to the accumulation of dead fishes on the strainer of the inlet. These fishes had seemingly been killed by the effluent from the tannery. The pH of the water is approximately 7.2 when in equilibrium with air. This shows a moderately high

bicarbonate content which would furnish a source for free carbon dioxide.

Observations on the carbon dioxide tensions and oxygen contents of river waters under natural conditions have brought forth some very interesting data (Powers and Hickman, '28; Powers, '28). It was found that the average carbon dioxide tension was .053 per cent of an atmosphere and the average oxygen content was 6.71 ml. per liter of all waters of rivers draining lakes. The waters of rivers not draining a lake had an average carbon dioxide tension of .115 per cent of an atmosphere and an oxygen content of 5.56 ml. per liter. The average difference in carbon dioxide tension between the two is .052 per cent of an atmosphere or one is practically double the other. This doubling of the carbon dioxide tension of drawn blood plasma is from equation $pH = pK_1 + \log[BiK/CO_2]$ sufficient to change its reaction over a range of .30 of a pH unit.

It has never yet been determined how a fish, such as a salmon, migrating up-stream adjusts itself to the differences in the physical and chemical characteristics of the two waters at the forks of a river. Is the response tropic or is there a rapid modification of its blood or both? It is quite obvious that all fishes do not respond in the same way. In any case a modification of the blood is a part of the final adjustment.

All recent observations point to the carbon dioxide tension and oxygen content of the water as important factors in the physiology of respiration of fishes. The carbon dioxide tensions to be investigated are those within the *a* range of the oxygen affinity curve of whole fish blood. The *b* and *c* ranges are of no significance when applied to the physiology of normal respiration of fishes.

SUMMARY

1. The loss of affinity of fish blood hemoglobin for oxygen at higher than normal carbon dioxide tension is not peculiar to fishes but is shared with hemoglobin of mammalian blood.

2. The isoelectric point of the hemoglobin of the yellow catfish is reached at a carbon dioxide tension of approximately .344 per cent of an atmosphere in blood of normal alkali reserve.

3. At carbon dioxide tensions of the blood from .344 per cent to 1.4 per cent of an atmosphere the hemoglobin increases in affinity for oxygen with rise in carbon dioxide tension.

4. At carbon dioxide tensions above 1.4 per cent of an atmosphere the hemoglobin again decreases in affinity for oxygen with rise in carbon dioxide tension.

5. An oxygen affinity curve has been drawn. It is concluded that the form of this oxygen affinity curve is modified by a change in the alkali reserve of the blood.

6. It is suggested that the epidemic of fish mortality in artificial ponds and natural waters is caused by the carbon dioxide tension of the water approaching a point sufficient to reach the isoelectric point of the hemoglobin.

7. This point is not often approached because of the small amount of oxygen dissolved in the water from which to derive carbon dioxide.

8. A very small sudden rise in carbon dioxide tension (50 to 100 per cent) in a stream is sufficient to kill salmon and fresh water fishes.

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THE EDGE OF THE FOREST IN ALASKA AND THE REASONS FOR ITS POSITION

Robert F. Griggs

George Washington University, Washington, D. C.

Transitions from one sort of vegetation to another—tension zones they have been called—are places of unusual interest to botanists. For along these lines, if they be in fact under tension from the struggles of diverse plants for ascendency, are afforded our best opportunities for unravelling the complex of factors which condition the success of the types concerned. Sometimes such vegetation lines, like the zones around a pond, are evidently due to transitions in physical or climatic conditions, each type of vegetation being clearly restricted to the habitat suitable to its own growth. In other cases the cause of the change in vegetation is not so readily apparent. Some of these obscure transitions are due to less obvious physical factors which may be made out by study or experiment. Others, conceivably at least, might represent actually moving migration fronts in no way related to physical factors. It was an attempt to gain an understanding of one of these more obscure boundaries that led to the present paper.

Among such tension zones the timber-line where trees give way to smaller plants holds a peculiar interest. When a resident of a forested region contemplates a treeless area, whether an isolated mountain peak that rises above timber-line or a general region like the Arctic vegetation zone, he is inevitably led to conjecture as to the factors which prevent the trees, aggressive invaders farther down, from penetrating into the bare area. The inevitable speculation thus aroused has led to the opinion commonly held that beyond the timber-line, temperature or some other physical factor is too severe for tree growth. It should be pointed out, however, that this opinion was reached many years before any critical examination of the facts of the case had been made. Perusal of the literature will indeed show that thorough studies of timber-line ecology are surprisingly few considering the great importance of the problem, both theoretical and practical.

It so happens that the edge of the forest in southwestern Alaska crosses the area devastated by Katmai volcano, whose great eruption it has been the writer's good fortune to study under the auspices of the National Geographic Society. During the fifteen years covered by the Katmai expeditions there has thus been afforded an exceptional opportunity for studying the forest boundary as a side line in connection with other researches into the eruption and its effect on vegetation.

Location of the Forest Front in Southwestern Alaska

The coasts adjacent to Katmai volcano, both on the Bering Sea and on the Pacific, are treeless [1] but the central portion of the Alaska peninsula at that point is occupied by a heavy forest of white spruce, *Picea canadensis* (Mill.) BSP. This forms the westernmost extension of the Hudsonian forest which stretches across the continent from Labrador.[2]

On the Pacific shore of the peninsula also are a few isolated clumps of spruce but these are Sitka spruce, *Picea sitchensis* Carr., instead of white spruce. That is, these are outliers not of the Hudsonian forest but of the coastal forest which stretches up from Oregon. One of these groves occurs on the unnamed cape which bisects Kuliak Bay. Another occupied a small islet in the mouth of Amalik Bay ten miles southwest. These trees were killed by the eruption but the largest had reached a diameter of two feet and supported an eagle's nest in its top.[3] Twenty miles farther west two small spruces about ten feet tall and perhaps fifteen years old were discovered in 1930 on the tundra near the northern entrance to Kashvik Bay. Finally, at Cape Kubugakli, is a clump of small spruces which look like offshoots from a single tree now cut down (see Cooper, '31). This clump constitutes the westernmost native Sitka spruce of which I have knowledge. Many years ago, however, the Russians planted a few trees at Unalaska, five hundred miles beyond Cape Kubugakli. These have continued to grow to this day. The isolated outliers on the Pacific shore of the peninsula seem more likely to have come from seed blown from Kodiak forty or fifty miles across Shelikof Strait than from the main body of the forest which terminates at Iniskin Bay, a hundred miles up the coast northeast of Kuliak Bay.

On the Kodiak Islands heavy forest, here a pure stand of Sitka spruce, reaches westward to a line extending from Black Cape on Afognak Island diagonally across Kupreanof Strait to Kodiak village. Beyond the main body of the forest are isolated outliers of greater or smaller dimensions as far as Uganik Island on the north and Ugak Island on the south. The village of Kodiak, the base from which the National Geographic expeditions carried on their work, is located almost precisely at the forest border. The village itself is treeless except where balsam poplars have been planted. But within half a mile to the northeastward heavy forest begins. It was around Kodiak that the study here reported was made (fig. 1).

[1] Forest in Alaska signifies "coniferous" forest. This is true both in common parlance and in the various publications such as the bulletins of the United States Geological Survey which have described the region. This paper, following the accepted usage, deals with the edge of the "spruce" forest. Beyond the spruces in places are balsam poplars (*Populus* species doubtful) and birches, *Betula kenaika*, which locally attain great size.

[2] This forest is shown in the picture on page 312 of the author's book, "The Valley of Ten Thousand Smokes," published by the National Geographic Society, 1922.

[3] Ibid. p. 330.

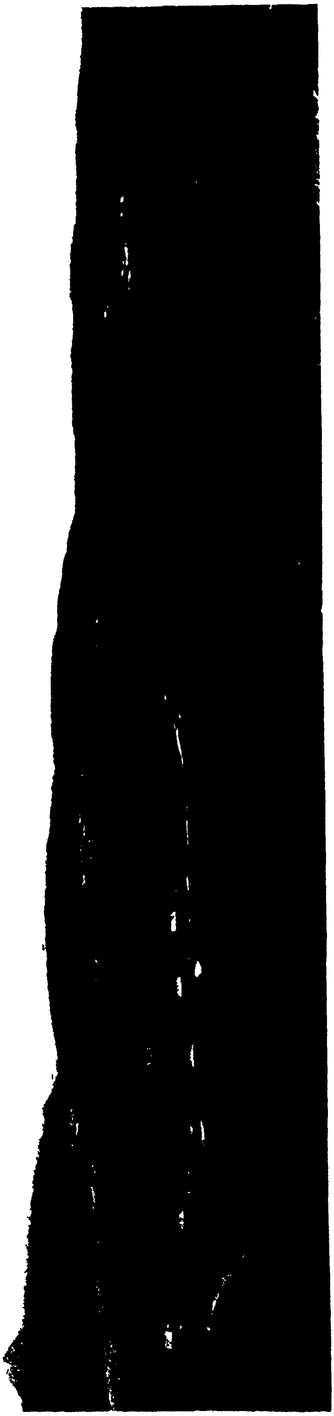

Fig. 1. The edge of the Forest at Kodiak. Continuous heavy forest at the right. Open grassland with scattering small spruces at left. Photo. by C. F. Maynard. 1917

Condition of the Trees at the Forest Front

An observer fresh from the magnificent forests of Oregon and Washington is likely to get an unfavorable impression of the spruces at the edge of the forest. They are low and squat, only thirty or forty feet tall. When growing together the tops of the individual trees are often lost in the general contour of the clump as though held to a dead level like the scrub along a wind-swept coast or the last trees fringing the streams on the plains. In short, one looking for indications of climatic control readily finds evidence in that direction.

But when one of the marginal trees was cut down and examined its growth rings made it seem doubtful that it had been held back by adverse conditions for whereas suppressed trees increase very slowly, the spruces at Kodiak were growing rapidly. Ten stumps counted at random gave an average growth ring of 0.098 inch. Individual rings occasionally exceed 0.5 inch. The largest measured was 0.57 inch. That is to say that the trunks sometimes had increased more than an inch in a single year. Farther back in the thick forest, growth is somewhat slower. Many stumps taken at random including overcrowded individuals and old slow-growing trees gave a general average of practically 0.08 inch per ring.

In order properly to evaluate these measurements information concerning the growth rate of the same species well within its range was sought. For this I am indebted to the officials of the Forest Service who have given me access to unpublished reports by R. F. Taylor on increment rates in second-growth forests in southeastern Alaska 700 to 1000 miles inside the limits of the spruce. Taylor's studies were made at 33 stations, mostly on the " Inside

Fig. 2. Spruce seedlings in the ash of Katmai. In many places such seedlings stand much thicker, but then grow less vigorously.

Passage" rather than on the outer coast. He subdivides the spruces into classes according to rapidity of growth, separating them into groups which at fifty years of age had attained heights of 30, 40, 50, 60, 70, 80, 90 and 100 feet respectively. The average growth rings for four intermediate classes probably give a fair picture of growth rates. These classes, computed from diameter-breast-high measurements, show increments at 30 years of .075, at 60 years .082, at 100 years .074, and at 150 years of .049 inches. Thus diameter growth at Kodiak appears to be fully up to the general average of the species.

The height increment of the trees of southeastern Alaska, on the other hand, is somewhat greater than of those at Kodiak, which, largely grown in the open, are low and bushy rather than tall and slender. Yet in height also the spruces at Kodiak make a fairly rapid growth. Normal trees regularly add six inches or more to their leaders every year. Vigorous young saplings often stretch up more than a foot per annum (fig. 2). In the light of these observations we had to conclude that so far as the vegetative processes are concerned the climate at the edge of the forest was not unfavorable to the spruce.

Reproduction of Marginal Trees

Our next inquiry concerned the reproductive functions. Here again, superficially at least, conditions seemed favorable. In each of the seven years that I have had opportunity to observe them the spruces at Kodiak have borne a heavy crop of cones (fig. 3). Apparently they fruit copiously every year.

Fig. 3. Cones on Sitka spruce at Kodiak.

But it is not the quantity of cones produced that is significant. Under climatic conditions too severe for the species, the fruit might be abundant but the seed defective. The real test of reproduction must be the viability of the seed. In this matter also examination revealed favorable conditions. The

seeds germinate freely and come up wherever they find suitable soil. In some places there were a hundred or more spruce seedlings per square foot on the new unoccupied surface of the volcanic ash. Everywhere on favorable soil they are much thicker than they can stand when they reach maturity (fig. 2).

With the demonstration that both vegetative and reproductive functions were going on normally the supposition that the limits of the forest are fixed by low temperature or other climatic factor loses its support. So far as can be seen the spruces might just as well as not occupy the treeless territory beyond their present boundaries.

As a matter of fact the evidence shows that the forest border is being actively extended by the invasion of the treeless zone.

Age of the Outermost Trees

The trees at the edge of the forest are small only because they are young. Those at the very edge are about 50 years old. Nowhere within a mile of the edge could I find a stump with more than a hundred rings. There are no fallen logs nor other evidence of trees older than those of the present forest.

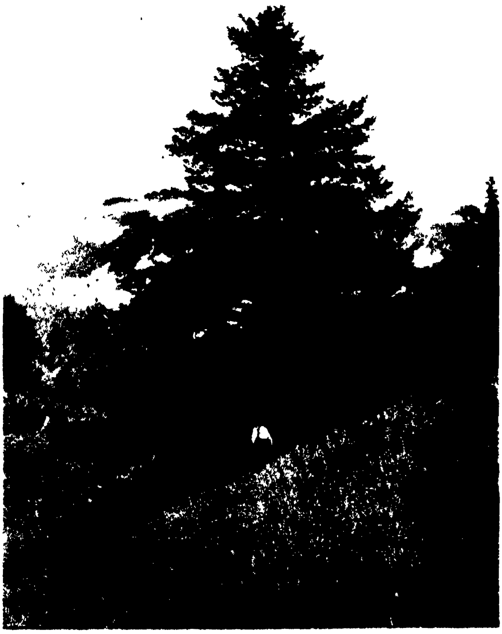

Fig. 4. The advance guard of the forest. Outlying trees coming up in grassland about five miles beyond the forest border.

The marginal trees are low and squat because, growing in the open, they have abundant light to the base, and their lower branches continue to elongate like "specimen" trees in a park instead of soon dying from over-shading as in the forest (fig. 4). In many cases these marginal trees stand at the center of a clump of young ones.

Back in the thick forest, moreover, there are many such mother trees whose heavy lower branches, now overshaded and killed by the growth that has come up around them, give the strongest testimony that they began life

FIG. 5. Mother tree, about 250 years old, surrounded by a thick forest of trees about 100 years old. About two miles back from the forest edge.

in the open like the present marginal trees and that during their own life time they have been overtaken by the advancing forest (fig. 5).

While there is no evidence of trees older than the present generation near the edge of the forest, about three miles back there are dead trees and fallen logs as in normal forests. Here the trees have reached great size, sometimes exceeding four feet in diameter. Many of them are tall and slender, evidently grown under forest conditions, but others, and these mostly older, still show the remnants of lower branches produced when they stood in the open.

The history of two stumps in this part of the forest is instructive. The first was 25 inches in diameter and 281 years old. It had required 35 years

to make the first 2.5 inches after which it had grown more vigorously till maturity. As it grew in rich well-drained soil its rings are interpreted to mean that it had a hard struggle at first with competitors, presumably other spruce saplings, but at 35 years succeeded in dominating its site and thereafter held its place in the growing forest canopy. The other tree was 36 inches in diameter and 38 years older (319 rings). But in these 38 years it had apparently been free from competition for it had grown four times as fast as its neighbor and reached a diameter of 10 inches. Thereafter it had slowed down somewhat but made normal growth for another century and a half after which it had increased but little, adding only two inches in the last 85 years. The bole of this tree was full of large knots clear to the ground which accorded with the testimony of the inner rings in showing that it had begun life in the open and grown for nearly 40 years before it began to show the effect of shade from neighboring trees. Clearly enough, then, this area, now about three miles within the forest, was at the margin three centuries ago.

The history of the trees thus unites with their growth and reproduction to deny that the forest is here held in check by any climatic factor and to testify that on the contrary it is advancing into new ground.

Absence of Human Interference with the Forest

In many places forest advances are occurring which are nothing more than recoveries from human interference with the course of nature. Darwin, for example, describes the transformation of a "barren heath" into a forest of Scotch pine by the simple process of fencing. The unfenced area where wandering cattle had free range appeared a perfectly natural formation presumably unable to support tree growth. But close examination revealed numerous seedling pines which were completely suppressed by grazing. We may surmise that such an area had been originally forest and that the trees merely regained possession when given a chance. Similarly parts of the prairie region of our own middle west come up to trees when seeds are available and fires are kept out. Some authorities have contended that the grasslands of North America have been carried far eastward from their natural boundaries by the prevalence of prairie fires which far antedated the coming of the white man. Others have contested this view and there is no occasion to open the question here. Yet there is a suggestion from an independent source that the prairies are not natural grasslands. Marbut has pointed out [4] that the soils of the eastern "prairies" as distinct from the more western "plains" correspond not to the soils of European grasslands but rather to soils which in Europe are occupied by forest. In the light of the possibility thus suggested that the prairies are partly man-made one could not attach much significance to their invasion by forest trees.

[4] Lecture before graduate school, United States Department of Agriculture. Mimeographed only.

No such complications occur in Alaska. Fires are unknown. From prehistoric times the country has been sparsely occupied by people without agricultural impulses or grazing animals whose living to a very large extent came from river and ocean. We are quite safe in dismissing human interference from the situation in Alaska and in looking at the forest advance as an event entirely within the orderly course of nature.

Early Records of the Forest at Kodiak

The rapidity of the change indicated by the trees themselves suggested that the former conditions ought to have been recorded by the earlier residents, for Kodiak is an old settlement dating back into the eighteenth century. This expectation turned out to be well founded. The harbor at Kodiak is formed by a group of small islands which protect it from the open ocean outside. The two largest of these are now called Wood or Woody Island and Long Island. As both are covered with heavy forest the appropriateness of the name Woody Island is not obvious. It turns out, however, that Long Island was formerly called Bare Island in contradistinction to Woody Island. This "Bare Island" was described by Davidson ('67) as having "the surface rolling and varied with herbage and a few scattering patches of trees."

Observation of forest conditions on Long Island in 1930 showed a situation similar to that near the forest front at Kodiak. There were many low-branched mother trees surrounded by younger growth. These were the oldest trees found. There were no fallen logs or old stumps. The oldest stump found had only 108 rings.

Far antedating the American tenancy is a description left by Martin Sauer, 1802, historian of the Billings expedition which visited Kodiak in 1790, who writes "In the interior they have good timber of common pine and on the eastern point of their island which Captain Cook called Cape Greville they have a very considerable forest of pines whence they bring the trees to build their huts and to repair their vessels." This point, Cape Chiniak, of present charts, is nearly 20 miles from Kodiak across an exposed bay difficult of navigation. It need hardly be added that no one in Kodiak would now think of bringing logs across this bay for the advance of the forest in the one hundred and forty years since this was written has provided plenty of acceptable timber within easy reach of the village.

Observation that the timber line of Kodiak is probably a moving front is, indeed, in no wise original to the writer but has been suggested by several previous authors. In the first comprehensive survey of Alaskan resources made under American auspices Petrof says: "On Kadiak Island and the Aliaska peninsula the change from a vigorous growth of spruce timber to bare hills and grassy plains is very abrupt and without any corresponding change in soil, temperature, or climatic conditions." Fernow ('02) on his visit to Kodiak with the Harriman expedition of 1898 first reported briefly the con-

ditions set forth in more detail in the present paper to the effect that the forest had migrated westward in recent years and was probably still on the move.

So far as Kodiak is concerned, then, the condition of the forest is certain. All lines of evidence converge to prove that during recent centuries it has been advancing into the area originally treeless. But the evidence so far considered gives no testimony as to conditions more than three hundred years ago. Moreover Kodiak is only one point along the thousand-mile forest front in Alaska. What of the rest of the line?

The Timber-line of the Alaska Peninsula

Fortunately the timber-line is so conspicuous and important a landmark that most explorers who have traversed it have made note of conditions there. The situation at Kodiak is not at all unique, for a number of those who have written about the subject have taken occasion to comment on the lack of any apparent reason for the present position of the forest front.

Osgood ('04) considered it hardly possible that there could be a significant

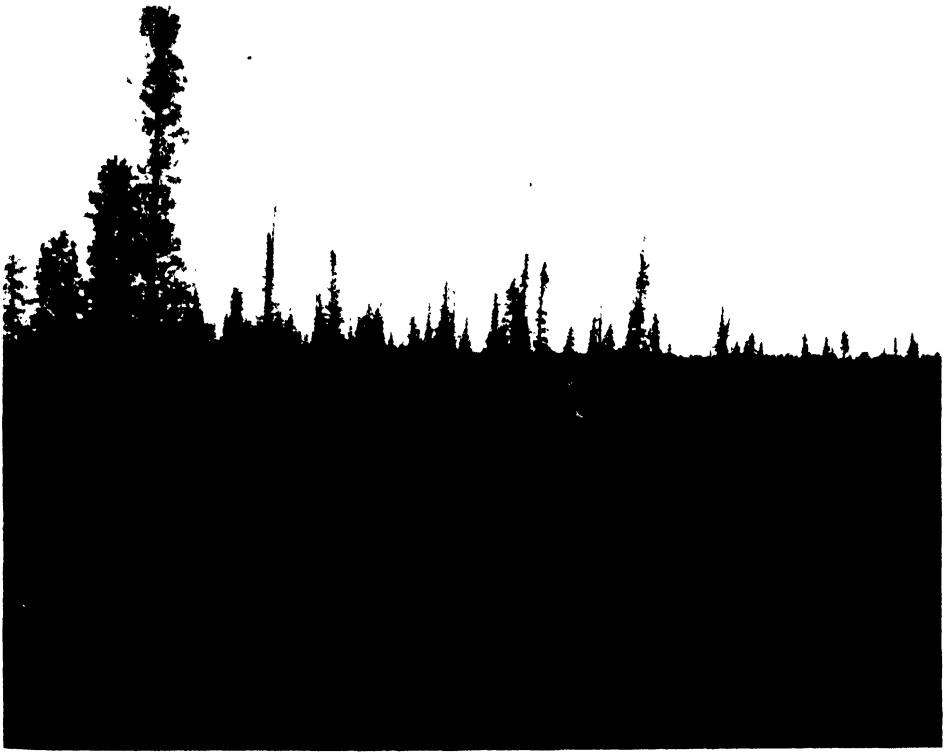

Fig. 6. Hudsonian forest of white spruce invading the tundra on the shore of lower Naknek Lake.

difference in temperature between the forested region around Lake Clark and the treeless area around Becharof Lake. He believed that more work would be necessary before the causes of the treelessness of the peninsula could be determined. Osgood's itinerary made a loop around the Katmai district, crossing from the Pacific to the Bering Sea through the forest *via* Iliamna Lake and back again via Becharof Lake in the tundra. Between the two lies Naknek Lake and the edge of the forest adjacent to the Valley of Ten Thousand Smokes. There was no opportunity for the National Geographic Society expeditions to carry on such detailed study here as that made at Kodiak. But the same conditions are indicated except that the advance of the Hudsonian forest of white spruce here is much slower than of the coastal forest at Kodiak. The trees near the forest border present the same appearance of vigor, grow well though not so fast as the Sitka spruce at Kodiak, and fruit copiously. All the trees are young and there are no remnants of a former generation (fig. 6). Martin and Katz's ('12) observations "support the conclusions of Fernow and Osgood that forests are now advancing into the treeless areas. The evidence for this lies chiefly in the scarcity of old dead trees throughout most of the forest areas and their complete absence on the margins of the forests."

The Forest Front in Western and Northern Alaska

Becker ('98) suggested that the reason the shores of Bering Sea are treeless might be that they had been lifted above the sea so recently that there had not yet been time for trees to colonize them.[5]

Of the central Kuskokwim Region, Lat. 62°, Long. 157°, Philip S. Smith ('17) says: "The spruce and birch at their upper limit are not exceedingly stunted as they usually are where their growth is controlled by climatic conditions, but the transition from the forested to the unforested areas is notably abrupt, as if the trees had not yet reached the limit imposed on them by their environment. This conclusion was suggested also by the lack of old dead trees near the margins of the forests." It is a curious fact that the altitude of timber-line is greater in some places along the northern border of the forest than farther south in regions of much milder climates. Thus Mertie ('25) reports in Lat. 68° "in some of the main valleys small timber continues upstream to altitudes of 3,000 feet or even higher. Thus timber is found for some distance above the forks of the North Fork of the Chandalar River up to an altitude of perhaps 3,200 feet." This is hard to understand when it is remembered that in south central Alaska, around Lat. 61° timber does not ascend above 2,000 or 2,500 feet even in great mountain masses like Mount McKinley.

Smith and Mertie ('30), summarizing the observations of several expeditions, say of northwestern Alaska: "In the valley of the Alatna spruce extends

[5] The geological part of this statement would not stand, I believe, in the light of later work but this does not affect the validity of the botanical part.

within about 6 miles of the pass to the Noatak and up the Unakserak to the camp of March 17. [Lat. approx. 67 degrees, 30 minutes, alt. 2600 ft.]. At both of these places the northern limit of trees comes abruptly. A few hundred yards south of the actual limit the trees are of about the same size as they are for scores of miles to the south but in that short distance they disappear entirely. On the Unakserak spruce trees 8 to 10 inches in diameter, 30 feet tall, and nearly straight, which apparently have suffered little from strong winds or cold climate, were found at Camp March 17, but 100 yards beyond there were not even dwarf trees or any signs that there had been trees for many miles. Plate 11A shows the last of the spruce that were seen on the Unakserak, and it will be noted that the trees are of good size as compared with the tents and are quite symmetrical. This same condition prevails on the Alatna above the Unakserak and when that region was surveyed in 1911 was described as follows: "The northern limit of trees is so sharply defined as to make a decidedly abrupt break which seems to have been controlled by some other factors than temperature and elevation." On the Noatak no spruce occurs anywhere east of longitude 161° 30′ or north of latitude 68° 13′. At the eastern limit of spruce in that valley the trees are 8 to 12 inches in diameter and grow as a narrow fringe along the well-drained river banks. Farther down the Noatak spruce is found almost everywhere in the lowland near the river to a point within a few miles of its mouth, where the ground becomes wet and spruce is absent. On the Noatak also the sudden disappearance of spruce is notable for in an earlier description of that region is the following statement: "The large size and sturdy growth of trees even near the borders of the unforested areas, is striking. Fully as large and vigorous trees were seen within 15 miles of the extreme limit of timber as anywhere else in the region although the place was fully as high, as much exposed, and had a soil not differing radically from that of the neighboring (unforested) tracts."

"Latitude is not the controlling feature in this distribution, for much of the eastern part of the Noatak basin lies south of the limit of spruce in the western part and some of it lies south of the latitude in which spruce on the Alatna and its tributary the Anakserak. On the Kuguruk River the expedition of 1925 found spruce extending within about 4 miles of Camp G April 26 or approximately to latitude 68° 13′ which is farther north than any other point at which spruce has hitherto been reported in northwestern Alaska."

The contrary opinion favoring the old conventional idea that the forest edge "must be" determined by climate is of course not lacking in the literature —though it is not put forward by those with extensive field experience in the region. Brockmann-Jerosch ('19) is sure that the cause of the colossal depression in timber-line by more than 10 degrees of latitude can be sought only in the character of the climate. Yet he is at a loss to put his finger on the factor concerned for he recognizes that "not one of the [climatic] factors is such as would, by itself, prevent tree growth." But instead of giving up the climatic hypothesis he falls back on an assumption that it must be the

complex of factors which is responsible and holds that "the climate is too oceanic." The fact is that like many another ecologist he is reasoning backward endeavoring to ascertain forest climates merely by observing the climate of timber-line, a procedure which would be valid enough if it were certain that the trees had pushed up to their climatic limits but of no validity at all where the forest is advancing.

In the light of the practically unanimous opinion of observers on the ground it seems justifiable to generalize and to conclude that in many places in Alaska the forest boundaries are mobile migration fronts rather than static climatic boundaries.

Irregularities in the Forest Front of Scandinavia

The essential unity of the circumpolar, boreal and arctic vegetation both ecologically and floristically suggested the advisability of inquiring concerning conditions at the edge of the forest in northern Europe. Upon looking up the matter we find that the botanists of Scandinavia have been as much perplexed as observers in Alaska by the irregularities in the position of the forest border. Conditions there as well as the various hypotheses that have been developed to explain them are summarized by Thore E. C. Fries ('13) p. 30ff. In the southern part of Scandinavia the spruce goes higher up the mountains than the pine, but in the north the reverse is true, the pine goes to greater altitudes than the spruce. Likewise in the lowland in Norwegian and Finnish Lapland the spruce drops out first and for a number of miles back from the northern border the forest is formed of pine only. But farther east in Russian Lapland spruce accompanies pines to the edge of the forest and in places goes beyond them forming the northernmost forest edge alone. The irregularities in the terminus of the Norway spruce have led to various conjectures as to their cause. Willkom supposed that the spruce was less injured by snow than the pine.[6] N. J. Anderson sought an explanation in irregularities of the heat effects of the sun on valleys presenting different exposures. Trautvetter and Hogborn assumed that there were biological races with varying powers of resistance to cold. Kihlman held that the pine was more resistant to fire than the spruce and attempted to account for the peculiarities by the forest fires of the last century. A new invasion he held was prevented because seed does not form in Lappmark. This appears to be the prevailing view at present.

Kjelgren and others, however, hold that the boundary is due to historical facts. It is maintained that the spruce is not so incapable of seeding along the edge as supposed and there is definite evidence of recent migration, to quote Fries (p. 41): "The spruce is continually pressing forward in northernmost Lapland toward the west. Its speed however is very slow because of the great resistance offered by the lichen-rich pine forest."

[6] Citation of authority for this and the following statements will be found in Fries's book.

Three facts militate against Kihlman's fire theory (1) The sharp boundary of the spruce forest which would presuppose rather recent fires along the whole boundary. (2) The complete absence of spruce from northern Lapland though it grows well when planted in Tromsö, Lat. 69° 30′. (3) " In the study of the fossil pollens of the bogs not a single pollen grain of spruce has been found while pine pollen is always common." [7]

Altogether these conditions along the border of the boreal forest of Europe are in no way inconsistent with what we have found in America. There are reports, however, that the forests of Eastern America and of Eastern Asia are retreating rather than advancing (See Frits Johansen 1919 and Middendorf 1864).

Is the Forest Advance Cyclic or Secular

There remains the question of the duration and nature of the forest advance. Evidence supplied by the trees themselves cannot take us back more than a few centuries. Is the present advance a relatively ephemeral episode due to a cycle of more favorable climate which will be reversed in another hundred years or so? Or is it a secular advance in the nature of recovery from the last era of glaciation? Is the unstable forest border slowly swinging back and forth like a pendulum now favored for a few hundred years, now driven back again by adverse conditions? Or are we witnesses to a permanent advance into new territory following the gradual improvement of climate through geological time? It is clear that if we can secure information on this point that we shall advance considerably in our understanding of the geological era in which we live.

It was because of inability to gain an insight into this aspect of the problem that I have held this paper since 1919 when most of the work was done. In the meantime methods have been developed for studying the vegetation of the geologically recent past by means of which it is possible to carry our knowledge of the history of the forest further back than is possible from the evidence above ground.

Testimony of Pollen from Kodiak Peat Bogs

Pollen analysis of peat has been developed to a point where it is capable of shedding much light on the former vegetation of a site. This method depends on the fact that the pollens which are blown into a bog resist decay and are preserved in the peat which accumulates from the vegetative parts of the bog plants. By appropriate means of maceration it is possible to eliminate the fibrous portion of the peat and concentrate the pollen grains lodged in any given layer. Then since the different pollens possess characteristic markings it is possible to determine to a considerable extent the plants which lived in the vicinity of the bog when the particular layer of peat was laid down.

[7] Quoted from Fries, p. 44.

One of the important side lines of the expedition of 1930 was therefore the securing of peat samples from bogs of the region. These have now been analyzed by my associate at George Washington University Dr. Paul W. Bowman, whose report of his findings is published herewith (pages 97–100). So far as the spruce is concerned the testimony of the pollen counts is clear and decisive.

The bogs from which the cores were taken are located at the heads of ponds about two miles inside the edge of the forest northeast of Kodiak. They are surrounded by heavy timber two or three hundred years old. They receive therefore quantities of spruce pollen at the present time.

The peat, however, carries only scattering grains of spruce pollen amounting to less than one per cent of the total spores present. Evidently the most recent peat antedates the present forest and the copious spruce pollen now showered into the bog every spring still remains in the unconsolidated debris on top of the peat. As is well known coniferous pollen is blown in quantity for long distances from its point of origin. The traces found in the Kodiak peat are much less than would have come from any nearby forest but are exactly what would be expected from the spruce forests on the mainland to the eastward.

Conclusions

The pollens in the peat very definitely then amplify the conclusions necessarily drawn from the conditions of the trees themselves and from the testimony of historians. They tell us not only that the forest has reached its present extension very recently but that the present are the first spruce trees that have grown around Kodiak since the beginning of the bogs. The advance of the forest demonstrated by the trees themselves is thus shown to be a long-term secular migration into new territory rather than a phase of a cyclic oscillation back and forth.

The interpretation of peat deposits has not advanced far enough as yet to permit any very definite opinion as to the period of time necessary for the accumulation of the eleven feet of peat found at Kodiak. The most that can be said is that this deposit has in all probability accumulated since the last glaciation. The peat does not therefore carry us back into the period of the fossil forest discovered by Cooper ('23), around Glacier Bay. Here an old forest was buried under many feet of gravels deposited during the last glaciation. These forests would seem to represent interglacial time in contrast to the postglacial history with which we are concerned at Kodiak.

In geological literature there are frequent suggestions that the northern hemisphere may not yet have recovered from the last glacial period. But botanists have given little thought to the possibility that vegetation might still be undergoing the readjustments consequent upon the retreat of the glaciers. The proof that in Alaska the forest is pushing forward into the tundra sug-

gests the advisability of examining other vegetation lines to see what sort of a story they will tell. What of other species on their northern boundaries; are they advancing or have they reached their limits? Are the well known glacial relicts of arctic vegetation on the mountains of New England stabilized or are they gradually losing out? Are the scores of boreal species which stretch far south along the eastern mountains holding their own or are they slowly receding?

The marginal individuals in all such cases should give decisive testimony for by studying these individuals which are in direct competition with plants of other formations it can be seen whether they are gaining or losing in the struggle. At the critical localities movements so slow that centuries would be required to effect significant changes in the position of boundaries may be detected readily and their direction determined. (See Griggs, 1914, McLaughlin, 1932.) The details involved in the examination of the matter are extremely numerous. But if we were in possession of the facts we should be able to construct from them a mosaic which would give us a conception of the age in which we are living far more accurate and perhaps quite different from that we now hold.

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POLLEN ANALYSIS OF KODIAK BOGS

Paul W. Bowman

The George Washington University, Washington, D. C.

During the summer of 1930 Dr. Robert F. Griggs was sent to Alaska by The National Geographic Society to study the return of vegetation over the areas around the volcano of Katmai which were heavily covered with ash during the eruption of 1912. While there he spent some time on Kodiak Island observing conditions along the edge of the forest. This island lies at the western side of the Gulf of Alaska at about 58° N. and 153° W. and is outside of the ash-covered area mentioned above. In this part of Alaska there is a definite edge to the forest, beyond which the country is treeless.

The evidence presented by Griggs in the preceding paper shows that the forest is advancing westward at an appreciable rate and strongly suggests that it is the first to cover this area since the melting of the last ice sheet. In the hope of obtaining definite evidence bearing on this problem, samples of peat were collected from two bogs located about two miles northeast of the town of Kodiak and within the forested area. To these samples the author has applied the methods of pollen analysis and has obtained results which indicate clearly that the forest is of recent origin and that there was none there during the time when the bulk of the peat in these bogs was accumulating.

For the benefit of those not familiar with the methods of pollen-analysis let us explain that during the accumulation of peat in a bog there settle over its surface each year countless spores, both from the plants growing in the area and from those in the surrounding country which are wind-pollinated. Many of these are well preserved in the peat and may for the most part be identified. As one analyses peat samples taken from the surface to the bottom of a bog so as to present a vertical section of the deposit he finds different kinds of spores and varying proportions of each kind at different levels. Thus are indicated the changes which have taken place in the vegetation of the region during the formation of the bog. Study of such observations has shed much light on the history of vegetation over northern Europe (Erdtman, '27, '30, '32) and is now being applied to similar problems in North America.

For a detailed study of the methods of pollen-analysis see Bowman ('31) and Erdtman ('33). In the present work the process was simplified by adding some safranin to the potassium hydroxide solution in which the peat was boiled. We prefer this stain to gentian violet, which was recommended in the earlier paper.

The two bogs mentioned are within a mile of each other. One is seven and the other thirteen feet deep. The upper three feet of peat were so wet and mushy that cores could not be taken with the peat sampler, but they were collected at one-foot intervals from the three-foot level to the bottom. These deposits are made up of numerous strata from each of which, as far as possible, a sample was taken for analysis. The number of pollen grains of each kind found at each level was recorded and is given in tables I and II where it is expressed as a percentage of the total number counted at that level. Where the quantity is reported as one per cent it should be interpreted as "a trace." Where none was found the space is left blank.

The pollen analysis shows that this peat accumulated during a time when there were few trees in the vicinity. Some alders were present when the formation of these bogs began. They disappeared, but later came in again and increased to such an extent that they contributed half of the pollen found in some samples. The birches increased from a trace to about 5 per cent, except for the greater quantity which was associated with the alder at the bottom of the seven-foot bog. A little poplar, a trace of willow and a few grains of spruce pollen were found. During the development of the bogs up to the three-foot level there seems to have been a decided lack of trees on or near them.

We very much regret that we do not have peat from the surface, analysis of which would complete the story, as the bogs are now located in a forest of spruce and hemlock.

On the strength of this evidence we believe that the forest now present at Kodiak could not have existed during the accumulation of the peat below the three-foot level, as we found only a trace of spruce pollen and no hemlock in this material. It is believed that spruce pollen, because of its form, can be carried much farther by the wind than hemlock, and it is quite possible that the few grains of it which were found might have been carried by the wind from trees a hundred miles or more away.

It is interesting to note that while the results obtained from the two bogs are essentially alike with respect to the items thus far discussed they are quite different in some other ways. The deeper one seems to have been much wetter than the other. In it at nearly all levels are found spores of *Nymphaea* and, in some strata, numerous diatom shells. Note that most of the spores found in both bogs, sometimes over 90 per cent, are those of some ferns. We do not yet venture to name these, but have designated them as A and B. In the deeper bog Fern B is found with A, and at times almost completely displaces it. The Cyperaceae and Ericaceae were more abundant over the seven-foot bog. Traces of *Lycopodium* and *Sphagnum* are found throughout both.

Summary

Pollen analyses of samples of peat from two bogs within the present forest edge at Kodiak, Alaska, show that during the time this material was accumulat-

TABLE I. *Pollen percentages in the seven-foot Peat bog*

Depth in feet	3	3.3	4	4.3	5	5.5	6	6.1	6.3	6.5	7
Alnus	15	9	14	13	8	7				4	11
Betula	5	4	3	3		1				2	8
Compositae				1	2					1	1
Cyperaceae	2	7	3	5	40	13	3	17	25	16	2
Ericaceae	4	2	4	15	5	3		2	2	2	27
Fern A	63	73	67	52	37	68	95	72	33	63	28
Gramineae				1	1	1				1	1
Lycopodium	1	1		1	1	1	2	5	1	1	1
Picea	1	1	1		1					1	1
Populus spp.				1	2					2	2
Salix spp.	1		1					1	3		1
Sphagnum spp.	2	1	4	2		1		1	1	2	11
Unknown	9	5	6	9	5	7	1	3	37	9	11
Number of spores counted	200	200	200	200	200	225	200	240	200	200	454
Relative density	57	43	20	74	14	225	1908	240	49	148	454

TABLE II. *Pollen percentages in the thirteen-foot Peat bog*

Depth in feet	3	3.3	4	4.5	5	5.5	6.2	6.3	6.5	7	7.2	7.4	7.45	7.5	8	8.1	8.2
Alnus	24	28	22	28	22	39	54	50	48	38	34	43	44	37	6	2	1
Betula	2	3	5	4	3	3	1	2	1	1	1	1	2	2	1	1	1
Compositae		1	1	1	1	1	1	1	1	1		1	1	1		1	1
Cyperaceae	7	1		1	1	1	1	1	1	1	1	2	2	1	1	1	2
Ericaceae	2	2	1	1	1	2	1		1	1	3	2	1	1	1	1	
Fern A	37	49	60	58	65	45	34	32	45	50	49	38	35	48	83	84	80
Fern B			2		1				1	1	1	1			1		6
Ferns, other	2	1	1		1					1			1	1		1	1
Gramineae	2	2	1	1	2	3	3	3	1	3	4	4	4	2	1	1	1
Lycopodium spp.	1	1	1	1	1	1	1	1		1	1	1	2	1	1	1	1
Nymphaea	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1
Picea	1	1	1	1	1	1	1										
Populus spp.	5	5	2	1			2	3		1		5	1	3	4	1	
Salix spp.	1	1				1		1			1						
Sphagnum spp.	1	1		1	1		1		1	1			1		1	1	2
Unknown	13	5	5	6	4	5	4	8	4	4	7	3	8	6	2	7	4
Number of spores counted	328	624	525	406	665	427	478	323	829	511	346	537	261	498	341	297	225
Relative density	10	312	262	203	332	213	239	20	414	255	69	179	29	249	170	20	75

Depth in feet	8.3	8.35	8.4	8.5	9	9.2	9.3	9.4	9.5	10	10.1	10.2	10.3	10.5	11	11.5	13
Alnus		1	1	2	1	1		1	2					1			34
Betula		1	1	1	1			1		1		1	1	1			1
Compositae							1	1		1			1	1			1
Cyperaceae	2	2	2	1	1	2	4	3	3	2	1	3	1	18	11	2	1
Ericaceae		1			1				1	1		1	1	4	3		1
Fern A	83	89	80	86	82	71	80	68	72	66	37	31	21	46	59	8	47
Fern B	3		3	1	5	12	1	11	7	20	52	60	75	2		85	5
Ferns, other	3	1	2	1			3			1	1				1		
Gramineae		1	1	1		1	1	1	1					1	1		
Lycopodium spp.		1	3		2	1	1		1	1		1		2	2		1
Nymphaea	3	1	1	1	5	4	2	4	5	3	3	1	1				1
Picea																	
Populus spp.	1		2				2	4	3	5	3	1	1		7		5
Salix spp.										1							
Sphagnum spp.		1	3			1		1		1		1	1	1	1	1	1
Unknown	7	4	4	7	4	10	9	7	7	2	4	4	2	25	17	5	5
Number of spores counted	200	229	200	292	303	340	203	342	367	420	363	716	825	247	231	643	349
Relative density	7	76	10	73	76	68	6	49	92	140	181	358	550	23	33	460	174

ing from the bottom to the three-foot level, above which samples were not obtained, there was a considerable increase in the amount of alder growing there and a slight increase in the quantity of birch. Traces of poplar and willow were found, and a few grains of spruce pollen.

We believe that this evidence shows that the edge of the forest at Kodiak has advanced from a point many miles to the east of the location of these bogs to a point a mile or more to the west of them during the accumulation of the upper three feet of peat.

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A BACTERIOLOGICAL STUDY OF FLATHEAD LAKE, MONTANA

V. E. Graham

University of Saskatchewan, Saskatoon, Saskatchewan

AND

R. T. Young

University of Montana, Missoula, Montana

A study of the physical, chemical and biological features of Flathead Lake has been under way for a number of years. This work was sponsored by the Fish and Game Commission of Montana and was carried out by members of the staff of the State University. The bacteriological work forming the basis of this report was done during 1929 and 1930.

A map of the lake is appended which shows its shape, the location of streams connected with it, the location of the " Stations " from which samples were taken and the names of towns and rivers referred to in the text. The lake covers approximately 189 square miles and has a maximum depth of 325 feet, the depth varying widely at different points. Its usual rise and fall is 10 to 13 feet annually. Since the bacteria of lakes in this region have not been studied extensively it is thought that the following notes may be of interest.

Methods

Bacteria counts were made by the plate method using nutrose agar (Fred *et al*, '24). Lake water agar, prepared by adding 1.5 per cent of agar to lake water was also tried on the suggestion of Dr. E. B. Fred. The counts obtained by the use of nutrose agar averaged 39 per cent higher than when lake water agar was used, and, therefore, nutrose agar was adopted for the work.

All counts were made after 25 days incubation at room temperature. A trial in which plates were counted after 15 days incubation and again after 25 days revealed an average increase of 9.3 per cent due to the longer period when nutrose agar was used. When lake water agar was employed there was no increase in count due to the longer incubation period, indicating that there was insufficient food material in this medium.

Samples of water were secured by use of the sampling device described by Wilson ('20). This device proved very satisfactory at all depths worked.

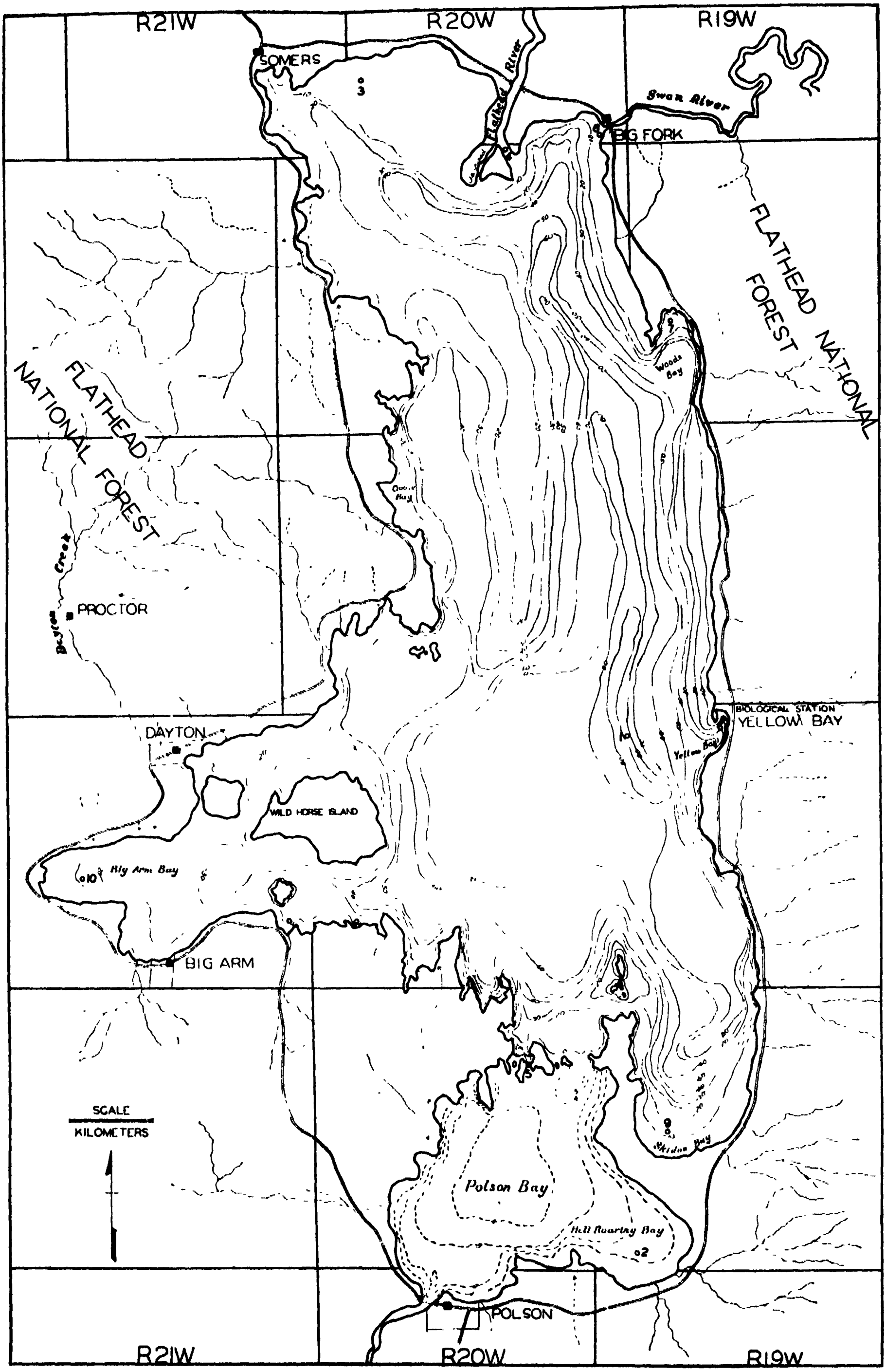

FIG. 1. Map of Flathead Lake, drawn by T. G. Swearingen, Maintenance Engineer, University of Montana. All depths are given in metres. The locations of the collecting stations (1–10) are indicated by circles.

TABLE I. *Bacteria per cc., Station 1, Flathead Lake*

Depth in feet	25.VI.1929	27.VI.1929	12.VI.1929	29.VII.1929	17.VIII.1929	27.IX.1929	12.X.1929	27.X.1929	9.XI.1929	29.XI.1929	19.XII.1929	2.II.1930	5.IV.1930	3.V.1930	1.VI.1930	20.VI.1930	Total	Average
0	191	22	57	77	133	1120	450	940	200	3300	120	40	130	16,050	380	4710	27,920	1745
5	19	23	103	48	17	90	1270	1080	290	260	220	30	50	3,270	—	—	5,627	483
10	80	84	173	120	384	70	620	270	200	530	50	120	360	1,540	—	—	4,601	328
20	100	117	169	203	124	110	710	240	320	180	20	10	30	2,150	—	—	4,483	320
30	145	133	107	62	69	40	480	180	60	60	30	150	130	1,600	—	350	3,576	238
40	89	66	81	71	255	50	610	10	970	30	110	90	20	870	—	—	3,322	237
50	17	63	126	92	81	240	1010	90	60	630	60	30	100	1,100	890	390	4,979	311
60	23	47	170	59	584	40	540	90	30	100	100	150	420	1,400	2110	1230	7,093	443
70	14	25	169	68	299	30	410	90	170	200	60	20	90	650	—	1800	4,095	273
80	36	32	129	56	66	0	340	380	220	140	160	70	300	1,780	—	1400	5,109	340
90	19	78	139	36	114	—	30	10	570	200	90	60	140	640	—	700	2,826	201
100	26	28	96	195	52	0	150	10	100	120	80	70	—	1,280	1060	970	4,297	286
200	22	23	92	47	35	—	90	180	30	60	—	70	30	1,120	820	20	2,639	189
280	18	20	82	89	35	0	840	80	120	50	30	—	—	780	—	—	2,154	179
Tot.	799	761	1693	1223	2248	1790	7550	4020	3340	5870	1130	910	1850	35,900	6230	11,550		
Ave.	57	54	121	87	160	149	539	265	238	419	87	70	150	2,445	1052	1283		

Some Factors Affecting Bacterial Life in the Lake

The pH of the water averaged about 8.35 and varied at different times and in different places within the limits 8.21 to 8.63. Howard ('29) ascribes the alkalinity of the lake chiefly to dissolved limestone.

Shallenberger ('29) studied the temperature variations in the lake during 1928 and presented the data shown in table III. These data were obtained at Station No. 1.

Howard ('29) found that the water of the lake was deficient in organic matter and that nitrites and nitrates were present in very small amounts.

Drainage of surface water into the lake was not an important factor during the summer of 1929 since this was one of the driest summers on record in this district.

Table II. *Distribution of bacteria with depth at all stations during period June 25–September 15, 1929*

Depth in feet	Station Number—(see Map) 1	2	3	4	5	6	7	8	9	10
0	96	768	617	716	242	69	60	6255	155	116
5	42	638	1085	660	291	112	165	7750	291	232
10	168			2620	161	93	106		129	192
20	143			4950 [1]	136	110	137		131	284
30	103				299	167	96		69	255
40	112				242	216	138		157	186
50	76				173	157	188		229	
60	177					108	66			
70	115					106	184			
80	64									
90	77									
100	79									
200	44									
280	48									

[1] Depth—15 feet.

Quantitative Results

To conserve space the stations have been grouped for discussion purposes into (*a*) deep water in the open lake, (*b*) shallow bays, (*c*) deep bays, and (*d*) river estuaries. Counts were made from the deep water Station (No. 1) at intervals throughout the year. At other stations counts were made only during July and August. There was thus no opportunity to study the seasonal distribution of bacteria except at the deep water station. No consistent differences were found in the counts at the stations within the groups mentioned above and the data presented represents the average count obtained at a given depth for all stations within the group. Table I contains all the data obtained at Station No. 1, with the date of collection.

Distribution with Depth. Samples of water from different parts of the lake varied widely in bacterial content. An average count of 4162 bacteria per cc. was obtained in samples from the river estuaries, the average at the Swan estuary being 6752, while an average of 2435 was found at the estuary

of the Flathead. This difference may be due to the presence of the small town of Big Fork near the mouth of the Swan river, and also to the fact that the Swan estuary is more shallow than that of the Flathead. The next highest average count was found in water from shallow bays, the average of all (16) samples being 1023 bacteria per cc. An average count of 220 bacteria per cc. was found in 18 samples from Station No. 5, which was located in a deep narrow channel. Deep bays showed an average count of 148 bacteria per cc. on 24 plates, while the average bacteria count on 70 plates from Station No. 1 was 96 per cc. during the same period.

An examination of table II reveals some relationships which may be significant, but which must be dealt with conservatively since the averages have been calculated from a small number of counts in some cases. In general there were fewer bacteria at the surface than at a depth of five feet. There are also indications of another point of increased concentration of bacteria at between 30 and 60 feet. Beyond this depth the count was lower. At Station No. 1 the average count throughout the year was higher at the surface than at a depth of five feet but this high average at the surface was due to a few high counts. These did not occur during the summer season.

It is suggested that the lower count at the surface than at a depth of five feet during midsummer is due to the greater intensity of light at the surface. Shallenberger ('29) found a decrease of about 25 per cent in the intensity of light transmitted through the surface, and a decrease of about 70 per cent at a depth of ten feet. Minder ('20) emphasized the effect of light upon the growth of bacteria in surface waters but Fred, Wilson and Davenport ('24) found no evidence of its influence.

Bacterial growth may also be influenced by temperature, reaction, and food supply. Fred *et al* ('24), and Minder ('20) found that the rate of multiplication of water bacteria was not greatly influenced by temperature. The temperature varied only slightly in the first five feet and Howard ('29) found no appreciable difference in the reaction and chemical composition of the water of the lake at different depths. These facts indicate that increased light intensity is chiefly responsible for the lower concentration of bacteria at the surface.

There may be another zone of increased bacterial activity at a depth of 30 to 60 feet. Shallenberger ('29) reported an increase in light absorption in the 30 to 40 foot zone but it is not clear whether the increased growth is the cause or the effect of the increased light absorption. In some cases there are indications of two zones of increased bacterial activity in the 30 to 60 foot layer. The temperature decreased more rapidly between the 20 and 60 foot levels, i.e., in the thermocline, than at other levels (table III). The plancton organisms in this and other lakes are also somewhat concentrated in the 30 to 60 foot levels.

Distribution with Season. There was a gradual increase in the counts obtained at all depths from June 25 to September 27, 1929. There was a

TABLE III. *Maximum and minimum temperatures of Flathead Lake, summer 1928*

Depth in feet	Degrees Centigrade	
	Max.	Min.
0	22.8	14.8
10	21.3	14.2
20	20.2	11.0
30	17.6	9.7
40	14.7	8.7
50	11.5	8.2
60	9.2	7.7
70	8.6	6.8
80	7.6	6.5
90	7.3	5.9
100	6.8	5.5
120	6.2	5.0
200	4.8	4.4
250	4.6	4.3
300	4.5	4.2

sudden increase on October 12 and the counts remained at a high level until November 29. The three counts made on December 19, February 2, and April 5, respectively, were comparatively low, while those made during May and June, 1930, were extremely high.

The summer of 1929 was extremely dry, but heavy rains fell during the autumn, which probably explains the high counts obtained at that time. During the winter of 1929–30 the snowfall in the mountains was particularly heavy and the precipitation was unusually large during April, May and June, 1930. The bacteria counts obtained would indicate that the amount of contamination from drainage water is a factor of first importance in determining the number of bacteria in the water of a lake of this size. To really determine the importance of this factor it would be necessary to continue the study over a period of years and also to determine the count at varying distances from the shore before and after rain had fallen. The weather conditions mentioned have been taken from the reports of the United States Weather Bureau at Polson.

Nitrification and Denitrification. Bacteria play an important rôle in the circulation of nitrogen in nature, breaking down the complex proteins of dead matter into the simpler forms of ammonia and nitrogen, and oxidizing these compounds into the form of nitrates, which form an important source of plant food. The growth of algae, weeds, and nitrate reducing bacteria, tends to reduce the supply of nitrates, while the activity of the nitrifying bacteria tends to increase the amount of nitrogen available in this form (Domogalla and Fred, '26). The data in table IV were obtained by inoculating tubes containing 10 cc. of potassium nitrate broth with 1 cc. of water taken from different levels at Station No. 1. It will be seen that the reduction of nitrates was very rapid, all but three tubes showing the presence of ammonia on the fifth day of incubation.

TABLE IV. *Denitrification of KNO_3 broth, inoculated August 30, 1929*

	31.VIII.1929		4.IX.1929		6.IX.1929		9.IX.1929		12.IX.1929	
Depth	NO_2	NH_3	NO_2	NH_3	NO_2	NH_3	NO_2	NH_3	NO_2	NH_3
0 ft.	—	—	—	—	—	—	—	—	—	—
5 ft.	+	—	+	+	+	+	+	+	+	+
10 ft.	—	—	—	—	—	—	—	—	—	—
20 ft.	—	—	—	+	—	+	—	+	—	+
30 ft.	—	—	+	—	+	—	+	+	+	+
40 ft.	+	—	+	+	+	+	+	+	+	+
50 ft.	+	—	+	+	+	+	+	+	+	+
60 ft.	—	—	—	+	—	+	—	+	—	+
70 ft.	—	—	—	+	—	+	—	+	—	+
80 ft.	—	—	—	+	—	+	—	+	—	+
90 ft.	—	—	—	+	—	+	—	+	—	+
100 ft.	—	—	—	+	—	+	—	+	—	+
200 ft.	—	—	—	+	—	+	—	+	—	+
280 ft.	+	—	+	+	—	+	—	+	—	+

An attempt was made to measure the activity of nitrifying organisms in the water by inoculating flasks containing 100 cc. of ammonium sulphate medium with water from the surface, 100 foot, and 200 foot levels. It was only possible to continue this experiment for 16 days and in this period neither nitrites nor nitrates were formed. This period was too short to show nitrification unless the process was being carried on vigorously. Fred ('26) found that the time required for nitrification to become evident, using equal amounts of inoculum and medium, varied from 12 to 30 days. Fred also points out that "Lakes with a low ammonia and organic nitrogen content . . . have a slower rate of nitrification." Since the water of Flathead Lake contains very small amounts of ammonia, organic nitrogen, nitrites and nitrates, vigorous nitrification could not be expected. It is possible that the shortage of nitrates is one factor responsible for the paucity of plant life in the lake.

Types of Bacteria Found in Flathead Lake

The bacterial flora of water is varied in character and subject to alteration from time to time. Bacteria from the soil and air, as well as animal and plant parasites and pathogens, frequently find their way into bodies of water. A heterogeneous group is, therefore, encountered, and it is difficult to determine which species and groups are indigenous to the water and which are really soil and air organisms. Under the conditions existing during the summer of 1929 this lake was unusually free from contamination from drainage water, a condition which makes it possible for the typical water forms to dominate the flora.

Chromogenesis. A larger proportion of colored colonies were obtained on nutrose agar than on lake water agar. When the results from all plates on which this character was especially noted were averaged it was found that 25.6 per cent of the colonies were colored. The percentage for Station No. 1

where the water was much deeper, and where one would expect to find a more complete dominance of water forms was 38.5. The distribution of these from top to bottom was remarkably uniform. Among the chromogenic colonies yellow and orange colors were by far the most prevalent. Red and pink colors of various shades were next in frequency. An occasional violet, blue and black colony was found but these were rare. There were some fluorescent colonies but no phosphorescent ones were noted.

Morphology and Cultural Characteristics. A large number of isolations were made but there was not sufficient time to study these completely. Of 32 of these cultures examined microscopically, 28 were small and medium sized rods, 3 were cocci and 1 was a spirillum. Spore formation was rarely noted. Of 26 cultures stained by Gram's method 8 were found to be positive and 18 negative. Only 6 cultures out of 29 were motile. Gelatine was liquefied by 16 cultures out of 45 examined, the incubation period being five weeks.

TABLE V. *Nitrogen analysis in parts per million*

Location	Date	Organic N	NH_3	NO_2	NO_3
Sta. 1 (Main Lake) surface	5.VII.1928	0.1548	0.062	0.0	0.0
Sta. 1 (Main Lake) 31 m.	5.VII.1928	0.138	0.108	tr.	0.0
Sta. 1 (Main Lake) 92 m.	5.VII.1928				
Sta. 2 (Hel-roaring Bay) surface	7.VII.1928	0.074	0.026	0.0	0.0
Sta. 5 (Narrows) surface	7.VII.1928	0.090	0.038	0.0	0.0
Sta. 5 (Narrows) 15 m.	7.VII.1928	0.132	0.048	0.0	0.0
Sta. 3 (Somers) surface	14.VII.1928	0.106	0.660	0.0	0.0
Sta. 4 (Mouth of Flathead River) surface	14.VII.1928	0.026	0.018	0.0	0.0
Sta. 4 (Mouth of Flathead River) surface	18.VI.1929	0.104	0.048	0.0	0.0
Average		.107	.131	tr	tr

This proportion of gelatine liquefiers is lower than that reported by Snow and Fred ('26) for the bacteria of Lake Mendota. Nitrates were reduced to nitrites by 21 cultures out of 47 examined. It has already been noted that nitrates were reduced vigorously by inoculation with lake water. Only 16 cultures out of 49 examined had any action on glucose, lactose or sucrose broths. Of these, 9 produced an acid and 7 an alkaline reaction. Gas production was not noted. The action of the cultures on litmus milk may be summarized thus: of 65 cultures examined 27 were without action on milk; 14 reduced the litmus; 6 digested the milk, 5 being alkaline digestion and 1 showing acid digestion; 2 cultures coagulated the milk, one being an acid coagulation and the other a coagulation of the rennet type; 3 cultures produced an acid reaction, and 23 produced an alkaline reaction.

Bacteria in Relation to Productivity

With the exception of a few species of bacteria, all animals and plants must depend upon organic matter in some form for their energy. In par-

ticular, animals must depend upon plants, and in most cases these must depend upon soluble organic compounds, nitrates, etc., for their food. It was found in this brief study that the waters of this lake were deficient in these respects. Periods of high bacteria counts were found, but during a considerable portion of the year bacterial activity seemed to be at a minimum. Smith ('31) has indicated that biological activity in natural waters may be stimulated by the addition of fertilizers, and his results would seem to warrant further work of this type to aid in increasing the productivity of lakes such as Flathead.

Summary

The results of a brief bacteriological survey of Flathead Lake, Montana, have been presented. The distribution of the bacteria in both space and time has been described.

Some of the important physiological and morphological characters of the bacteria of the lake are also reported, together with a brief study of nitrification and denitrification. Further studies of this nature on lake water should yield valuable information regarding the relationship between bacteria and their environment.

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VULNERABILITY OF BOB-WHITE POPULATIONS TO PREDATION

Paul L. Errington

Iowa State College, Ames, Iowa

McAtee ('32), generalizing from the results of 80,000 bird stomach examinations, concludes broadly that predation tends to be proportional to population. Later, in a recent paper, he modifies his conclusion, ". . . the proportion, however, rising and falling progressively with the increase or decrease in numbers of the available food organisms" (personal letter, October 14, 1933). My data on Wisconsin Bob-White (*Colinus virginianus virginianus* Linn.) populations suggest a further elaboration of this thesis, namely, that predation seems to vary with the ratio between population and the carrying capacity of the environment.

This paper is mainly an analysis of data derived from two to four years continuous field investigation, the primary object of which was to ascertain the extent and the causes of quail mortality in environments typical of those to be found in many of the north-central states. For detailed area data and description of techniques, reference is made to Errington ('33c). Additional work in Iowa and Minnesota supplement that done in Wisconsin (Errington, '33d).

Recent publications (Stoddard, '31; Errington, '31a; '31b; '32b; '33b; '33c; Leopold, '33) dealing with bob-white population levels and predation upon the species have taken a distinctly ecological approach, but they fall short of furnishing more than fragmentary glimpses of the ecological picture. Similarly, nesting studies (Stoddard, '31; Errington, '33e) have given more glimpses to be interpreted as best they may. These studies have made plain certain correlations between the character of the environment—particularly, as regards food and cover—and predation upon bob-white populations.

It is not enough, however, to establish fairly well that so many birds of a given population survived the winter, or that so many starved, so many were killed by Cooper's Hawks (*Accipiter cooperi*), so many by great Horned Owls (*Bubo virginianus*), etc., nor is it enough to state with accuracy that quail made up a certain percentage of a predatory species' diet or that quail were taken by an individual predator at the rate of so many per given unit of time. Neither is it enough to arrive at something of an understanding as to why predation upon bob-white may be high or low for a given predator species under given conditions. Indispensable as these data may be to a thorough investigation, yet they constitute only groundwork. We need to go farther,

not wholly as an indefinite continuance of observational or experimental routine, but to attempt to extract some more coherent meaning from the work so far done.

Briefly, the present data indicate that there is room for only about so much of a winter bob-white population in north-central states environment. Each tract of land has a number of combinations of food and cover, each combination offering habitable winter territory for a quail covey. The number and quality of these combinations or territories determines the number of quail normally resident. Under stable agriculture, the resident population does not change greatly from year to year, save when reduced as by over-shooting or by some natural catastrophe as a blizzard or sleet storm of extraordinary severity.

When a series of mild or snowless winters coupled with sufficiently favorable breeding seasons permits the filling up of habitable quail environment and forces the spread of population into environment marginal for the species, an acceleration of predation occurs tending to trim down the excess to the normal population. Conversely should the bob-white population level for some reason be lower than the carrying capacity of the land, the predation rate is greatly lessened. In other words, if a quail population fits well into an environment it suffers light or negligible loss from predation; if the environment is weak for the population the latter will suffer to the extent of its vulnerability.

Environmental Carrying Capacity for Quail

The carrying capacity of an environment, for purposes of this paper, may be taken as the heaviest quail population which it may be expected to winter. This, in short, means the maximum seed stock by about April 1, or the time when birds begin splitting from coveys and pairing preliminary to breeding. Expressed otherwise, carrying capacity decides that there shall be no more than about so many winter survivors; it provides no assurance that such a number will survive. Populations actually wintering may fluctuate according to irregular availability of food, emergencies of many sorts, poaching, etc. Sudden starvation mortality, for instance, may deplete populations much below carrying capacity.

The more extensive the areas under observation the more correctly carrying capacities may be calculated. Population densities graduate downward from the apparent saturation point of a bird per acre (Stoddard, '31; Leopold, '31). Environment at the fringe of the range may not have definable carrying capacity because of the precarious status of bob-white populations there and their consequently vacillating population densities. Hence generalizations as to carrying capacities should be based upon data from environments of enough average uniformity to hold populations at somewhere near constant levels during the winters of moderate severity that the birds usually experience in accepted northern quail range. Data from the majority of the south-central Wisconsin

observational areas for the years given appear, from this point of view, to be fully eligible for use.

The Wisconsin observational areas will be lettered for convenience as in the paper already referred to (Errington, '33c). Area "G," by virtue of its large size and the amount of work done here for four years from 1929 to 1933, may be offered as the leading observational area, and data from this source may conceivably be worth more than from all the others together. Careful studies have been conducted on smaller areas also and for which, except as stated, the data may be adjudged scientifically acceptable. In nearly all cases census and mortality figures have been arrived at with reasonable accuracy, and as much consideration as possible has been given the values of salient ecological factors such as quality and distribution of food and cover, climatic emergencies, kinds and abundance of predators, and, quite roughly, the kinds and abundance of quail competitors and buffer species. Studies of bob-white behavior, especially as related to covey composition and movements, comprised an integral part of the research (Errington, '33a; '33c).

It may be appropriate to remark in advance that precise winter quail counts are made with increasing difficulty as April approaches; in fact, most coveys cannot be kept under satisfactory observation as long as this. When it has proved impossible to follow the fortunes of a covey up to this date, gaps have been filled in by computing losses past the actual census dates on a pro-rata basis.

Granted that the construction of a complete ecological picture is impossible, if for no reasons other than human limitations in fact-finding and fact-interpretation and the vast array of variables always operative, still it my be profitable to consider the available data in their broader aspects, apart from the confusing intricacy of solved and unsolved detail.

Area " G " east of Prairie du Sac, Wisconsin—3200 acres

Winter	Population		Total Losses	Density (bird : acres)	
	December	April 1		December	April 1
1929–30	121	112	9	1 : 26.4	1 : 28.5
1930–31	257	236	21	1 : 12.5	1 : 13.6
1931–32	400	290	110	1 : 8	1 : 11
1932–33	406	339	67	1 : 7.9	1 : 9.4

At the time when the Wisconsin investigation was started, July, 1929, quail populations in the south-central part of the state were recovering from a rather wholesale decimation attending the preceding winter's heavy and persistent snows. Accordingly, in area " G " as in the following, the initial observations had to do with an ascending but distinctly low quail density.

The losses listed may be regarded as normal with the exception of a 1931–32 late winter starvation mortality of around 39 birds; insofar as these had practically wintered it seems evident that except for the emergency the survival

would have been in the vicinity of 329 or one per 9.7 acres. This 1 : 9.7 correction substituted for the third year spring density of 1 : 11 (last column) together with the 1 : 9.4 fourth year spring density, point to a normal equilibrium level of about a bird per 10 acres, *i.e.*, the carrying capacity of the area in its present vegetative condition.

Area " C " north of McFarland, Wisconsin—1280 acres

Winter	Population		Total Losses	Density	
	December	April 1		December	April 1
1929–30	32	18	14	1 : 40	1 : 71
1930–31	21	20	1	1 : 61	1 : 64

Farmers say the locality always has had a sparse quail population; while they are prone to lay the blame on pot-shooting, in actuality the two rather uniform area " C " spring survivals suggest instead a very low environmental carrying capacity. None of the 1929–31 losses were traced to shooting.

Area " D," west of Pine Bluff, Wisconsin—640 acres

Winter	Population		Total Losses	Density	
	December	April 1		December	April 1
1929–30	36 +	22	14 +	1 : 17.7	1 : 29.1
1930–31	32	31	1	1 : 20	1 : 20.6
1931–32	63	35	28	1 : 10	1 : 18.3

Area " F," east of Pine Bluff, Wisconsin—640 acres

1929–30	25 +	10	15 +	1 : 25.6	1 : 64
1930–31	38	32	6	1 : 16.8	1 : 20
1931–32	54	39	15	1 : 11.9	1 : 16.4

Areas " D " and " F " were located about three miles apart and in the same type of country. Neither population in 1929–30 was located for study until late January; both lost severely from starvation the first season, which losses, except for 8 starving on area " D " in 1931–32, constitute practically the only mortality not to be looked upon as normal. The starvation mortality was due to a crisis precipitated by cold weather accompanied by snow deep enough to cut off a previously adequate food supply; had it not been for this the 1929–30 spring survival for " D " should have been something like 32 birds or one

Area " A," Wingra Wild Life Refuge, Madison Wisconsin—200 acres

Winter	Population		Total Losses	Density	
	December	April 1		December	April 1
1929–30	37	23	14	1 : 5.4	1 : 8.7
1930–31	67	58	9	1 : 3	1 : 3.4
1931–32	70	46	24	1 : 2.9	1 : 4.3
1932–33	41	41	0	1 : 4.8	1 : 4.8

per 20 acres and for " F," 25 birds (possibly more, as they were starving when discovered) or 1 per 25 acres. Substitution of these figures for the actual 1929–30 spring survivals would bring all spring survivals for the two areas near a mean of a bird per 20 acres or carrying capacity.

Only one of the birds lost in 1929–30 was known to succumb to causes other than a late season starvation, practically after the winter was over, hence, the normal survival should have been about 35 birds or one per 5.7 acres. The emergency mortality of 1931–32 (a March blizzard killed or caused to leave about 22 of a population which prior to the blizzard had wintered with but two lost birds) nevertheless, if classed as abnormal, would indicate an expected survival of 68 birds or one per 3 acres. The carrying capacity of area " A," then, appears to vary around a bird per 5 acres, though this figure is not any too satisfactory and probably is the least constant for any observational area.

Emergency conditions may greatly complicate efforts to judge carrying capacity. During the winter of 1929–30 the population of area " E " mostly starved out, as a consequence of which the surviving seed stock amounted to no more than 12 birds, or one per 80 acres. The next season 33 birds wintered, or one per 29 acres; in 1931–32, 77 or one per 12.5 acres were easily accommodated until the forepart of March, when the belated cold and snow brought an unmeasured but apparently not drastic mortality. On its qualifications, this area may have a carrying capacity, aside from the emergency variable, as high as a bird per 2 or 3 acres. Likewise, area " H " in 1931–32 had comfortably wintered around 85 birds or one per 4.7 acres until the March vicissitudes wiped out a full 80 per cent of the population in a couple of weeks.

Area " B " produced data on carrying capacity which look significant from a somewhat different angle. In 1929–30 the average population was 20 quail and about 12 ring-necked pheasants (*Phasianus colchicus torquatus*). In 1930–31, 47 quail and about 30 pheasants represented the population, or one quail per 4.2 acres and one pheasant per 6.7 acres, a combined gallinaceous stand of a bird per 2.6 acres. The next winter the area supported 26 quail and about 50 pheasants, or one quail per 7.7 acres and one pheasant per 4 acres; combined, one gallinaceous bird per 2.6 acres, as before. The carrying capacity was abruptly lowered for the winter of 1932–33 by plowing and cleaning up of so much of the agricultural land that virtually no food was available except around farmyards—not even enough food to make up habitable fall covey territories! No quail were regularly resident on the area, and but 12 pheasants were counted.

Wisconsin field notes furnish data on at least 22 specific quail environments (as distinguished from the observational areas) used by coveys or covey groups for observational periods of two seasons or more. Reference is restricted to environments for which the winter food and cover balance has remained essentially unchanged, season to season, except for minor changes on account of crop rotation, and similar human activities.

Of the 22 specific environments, for which data from two to four years are recorded, 20 may be classed as simple wintering territories. Of these 20, it may be said that 16 exhibited a fairly distinct season-to-season constancy of carrying capacity, although the carrying capacities varied with the individual areas.

Fully occupied territories, irrespective of initial early season populations, commonly wintered maxima of only about so many birds. Typical actual survival figures for successive winters on specific quail territories: 21–22; 14–20–15–15; 20–16–20; 17–7 (atypical because of highly unusual circumstances)—17; 23 (reduced by late winter starvation, hence atypical)—32–29–33; 12–0 (territory not occupied this season)—13; 11–11–12; 30–32; 7 (territory not fully occupied)—16–19.

Carrying capacities of Iowa quail environments tentatively listed on the basis of one year's field work are: Des Moines city waterworks supply grounds (1400 acres), one bird per 8.3 acres; Ledges State Park, Boone (500 acres), one per 11.4; farm land adjacent to Ames (1500 acres), one per 10.2; farm land south of Grinnell (1 sq. mile) about one per 15; farm land north of Mt. Vernon (4 sq. miles) about one per 25; Ft. Des Moines state game management area (1 sq. mile) up to one bird per 2 acres or higher.

Kendeigh ('33, p. 5) computes from the annual late December Bird Lore censuses the average density of Ohio bob-white populations to be one bird per 10.9 acres for the closed season years of 1913 to 1931. This would denote a carrying capacity of a bird per 13 [1] acres, perhaps not so far also from the average for southern Iowa and for superior southern Wisconsin quail country.

Carrying capacity evidently is a real property of environments and serves to delimit populations rather than to insure their numerical status, although populations within regular quail range have a way of keeping habitable environment quite well filled up, when not forced down by excessive shooting or by severe climatic emergencies. Carrying capacity, too, appears characterized by a degree of constancy from one year to the next unless either raised or lowered by human manipulation or by ecological succession, fire, etc. Certain competitors for the essential constituents of the environment—territory in particular—may also exert material influence.

Predation in Relation to Bob-White Population Densities

As already stated, the data from my quail studies seem to support a modification of McAtee's ('32) proportional predation thesis, in that the rate of predation upon winter bob-white populations remains low and fairly constant

[1] Kendeigh's ('33, p. 14) calculated annual surplus of 39 per cent points to conditions comparable to those of area "G" in 1931–32 which showed a 12.5 per cent winter predation rate per 90 days. This would reduce a bird per 10.9 acres population to a bird per 13 acres from New Year's to April.

until those populations reach the carrying capacity of the land, but rises abruptly (table I and fig. 1) for populations exceeding carrying capacity.

Table I gives the available predation rate data standardized for comparison with percentage figures used to designate the degree to which bob-white populations filled up environments under observation. Percentages of stocking refer to the proportion of population to carrying capacity.

TABLE I. *Tabular standardization of predation data*

Area	Season	Percentage stocked with quail	Actual predation rate	Pro-rata percentage predation rate for 90 days
G	1929–30	38	5% in 77 days	5.8
	1930–31	80	5% in 83 days	5.4
	1931–32	125	15.3% in 110 days	12.5
	1932–33	127	15% in 106 days	12.7
C	1929–30	160	25% in 107 days	20.8
	1930–31	105	5% in 80 days	5.6
E	1929–30	9 (?)	None (?) in 75 days	0.0
(Est.	1930–31	11 (?)	2.3% in 70 days	2.9
c.c.	1931–32	20 (?)	1.3% in 90 days	1.3
1:2.5)				
D	1929–30	112	2.8% (?) in 61 days	4.1
	1930–31	100	3.1% in 96 days	2.9
	1931–32	197	19% in 70 days	24.4
F	1929–30	78	None in 20 days	0.0
	1930–31	119	10.5 in 71 days	13.3
	1931–32	169	18.5% (?) in 78 days	21.4
H	1931–32	45 (?)	5.5% in 75 days	6.6
A	1929–30	93 (?)	2.7% in 92 days	2.6
	1930–31	168 (?)	12% (?) in 99 days	10.9
	1931–32	175 (?)	2.9% in 75 days	3.5
	1932–33	103 (?)	None in 41 days	0.0
B	1929–30	26	None in 80 days	0.0
	1930–31	61	None in 70 days	0.0
	1931–32	34	None in 70 days	0.0
Ia.1[1]	1932–33	107	6.8% (?) in 95 days	6.4
Ia.2[1]	1932–33	118	11.5% (?) in 96 days	10.8
Ia.3[1]	1932–33	120	6.8% in 95 days	6.4
Ia.4[1]	1932–33	36 (?)	6% (?) in 80 days	6.8

[1] Ia.1 means Des Moines Waterworks area; Ia.2, Ledges State Park; Ia.3, Ames; Ia.4, Ft. Des Moines.

In analyzing the data it has been necessary to segregate predation from other winter losses. Mortality from specific predators on the observational areas has been more or less satisfactorily established in a large number of cases through scrutiny of the evidence left from kills and through food habits studies of the predators themselves (Errington, '32a). Where the evidence has been less tangible, I have been compelled to interpolate into the sound predation

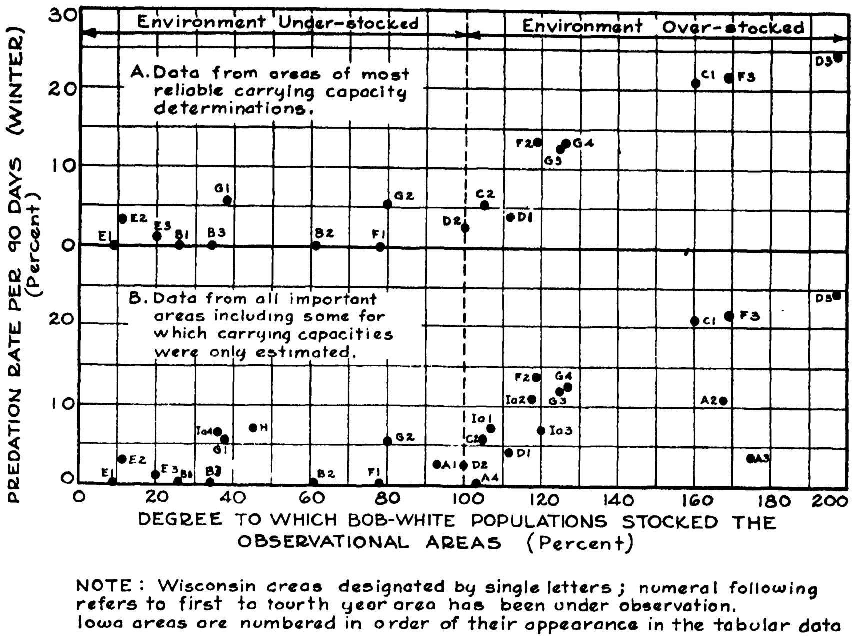

FIG. 1. Rise of predation rate on bob-white populations ascending past the carrying capacity of the environment.

data values based upon birds missing from healthy coveys where the presumption of starvation losses would have been improbable; this permits some unknown losses from poaching or accident to be charged to predation, but the resulting possible error, as checked by the most accurate area data, does not at present appear serious.

Not included under predation losses are kills by predators of quail helpless or dying from starvation or from other causes that would obviously have eliminated them anyway. For instance, quail of area " E " in 1929–30 and area " H " in 1931–32, from evidence in the snow, were known to have been starving when caught by Red-tailed (*Buteo borealis*) and Marsh Hawks (*Circus hudsonius*) (Errington, '33c). It is evident that such losses do not reflect predation in a normal sense, and are not to be confused with losses of strong though perhaps vulnerably situated birds.

The reduction of quail populations in excess of carrying capacity in the Wisconsin areas was commonly brought about through the medium of predation, but it does not follow that predation has a corresponding effect in determining population levels. Neither does it follow that the net amount of predation is dependent upon the kinds and densities of predatory species. This is evinced by table II, a critical examination of which may reveal very little to support some ideas generally entertained.

While table II is specifically recommended to readers desirous of checking

TABLE II. *Summary of 1929–1933 winter quail observational area data with reference to predation*

Area	Quail density	Rate of predation	Buffer [1] population	Predators present in av. covey territory. + signifies extra heavy density
"G" 3200 acres. Calc. carrying capacity 320 or 1 : 10	121 or 1 : 26.4 (1929–30)	6 or 5%. Av. 77 days	Mm heavy + Dm ? Ct mod. SB mod.	Common visitors: Horned and Barred Owls, Redtailed Hawk, House Cat. Occasional: Grey Fox, Weasel
	257 or 1 : 12.5 (1930–31)	13 or 5%. Av. 83 days	Mm light Dm mod. Ct mod. SB mod.	Common visitors: Horned Owl, Cooper's and Redtailed Hawks, House Cat, Grey Fox, Weasel. Occasional: Barred Owl
	400 or 1 : 8 (1931–32)	61 or 15.3%. Av. 110 days	Mm light Dm heavy Ct mod. SB light	Daily visitors: Grey Fox. Common: Horned Owl, Redtailed Hawk, House Cat, Weasel. Occasional: Barred Owl, Mink
	406 or 1 : 7.9 (1932–33)	61 or 15%. Av. 106 days	Mm mod. Dm mod. Ct mod. SB mod.	Daily visitors: Grey Fox +. Common: Horned Owl, Redtailed Hawk, House Cat, Weasel. Occasional: Barred Owl, Cooper's Hawk
"C" 1280 acres. Calc. carrying capacity 20 or 1 : 64	32 or 1 : 40 (1929–30)	8 or 25%. Av. 107 days	Mm heavy + Dm mod. Ct mod. SB mod.	Daily visitors: Marsh Hawk. Common: Redtailed Hawk, House Cat, Weasel
	21 or 1 : 61 (1930–31)	1 or 5%. Av. 80 days	Mm light Dm mod. Ct mod. SB mod.	Common visitors: Redtailed Hawk, House Cat. Occasional: Horned Owl, Weasel
"E" 960 acres. Est. carrying capacity 320 to 480 or 1 : 3 or 2	37 or 1 : 28.6 (1929–30)	None ? Av. 75 days	Mm heavy + Dm ? Ct light SB mod.	Common visitors: Redtailed Hawk, House Cat. Occasional: Mink
	44 or 1 : 21.8 (1930–31)	1 or 2.3%. Av. 70 days	Mm light Dm mod. Ct mod. SB mod.	Common visitors: Barred Owl, Weasel. Occasional: Horned Owl, Redtailed and Cooper's Hawks, House Cat, Mink
	78 or 1 : 12.3 (1931–32)	1 or 1.3%. Av. 90 days	Mm light Dm mod. Ct mod. SB light	Daily visitors: Barred Owl, Redtailed Hawk, Weasel. Common: Horned Owl, Grey Fox, House Cat, Mink
"D" 640 acres. Calc. carrying capacity 32 or 1 : 20	36 or 1 : 17.7 (1929–30)	At least 1 or 2.8%. Av. 61 days	Mm heavy + Dm mod. Ct mod. SB mod.	Daily visitors: Horned Owl, Redtailed Hawk, Weasel. Common: Red and Grey Foxes
	32 or 1 : 20 (1930–31)	1 or 3.1%. Av. 96 days	Mm light Dm mod. Ct mod. SB ?	Daily visitors: Horned Owl, Redtailed Hawk, Grey Fox, House Cat, Weasel. Common: Barred Owl, Red Fox. Occasional: Cooper's and Marsh Hawks

[1] Meadowmouse is abbreviated in buffer column to Mm; deermouse, Dm; cottontail rabbit, Ct; small birds, SB.

TABLE II.—*Continued*

Area	Quail density	Rate of predation	Buffer population	Predators present in av. covey territory. + signifies extra heavy density
	63 or 1 : 10 (1931–32)	12 or 19%. Av. 70 days	Mm light Dm heavy Ct heavy SB ?	Daily visitors: Horned Owl, Redtailed Hawk, Grey Fox. Common: House Cat, Weasel. Occasional: Mink
"F" 640 acres. Calc. carrying capacity 32 or 1 : 20	25 or 1 : 25.6 (1929–30)	None in 20 days	Mm heavy + Dm mod. Ct mod. SB heavy	Daily visitors: Grey Fox, Weasel. Common: Redtailed Hawk, House Cat. Occasional: Horned Owl
	38 or 1 : 16.8 (1930–31)	4 or 10.5%. Av. 71 days	Mm light Dm mod. Ct mod. SB mod.	Daily visitors: Grey Fox, Weasel. Common: Horned Owl, Redtailed Hawk, Red Fox, House Cat. Occasional: Cooper's Hawk, Mink
	54 or 1 : 11.9 (1931–32)	About 10 or 18.5%. Av. 78 days	Mm light Dm heavy Ct mod. SB ?	Daily visitors: Grey Fox, Weasel, House Cat. Common: Redtailed Hawk, Mink. Occasional: Marsh Hawk
"H" 400 acres. Est. carrying capacity 200 or 1 : 2	90 or 1 : 4.4 (1931–32)	About 5 or 5.5%. Av. 75 days	Mm light Dm mod. Ct mod. SB ?	Daily visitors: Marsh Hawk, House Cat. Occasional: Horned and Barred Owls, Redtailed Hawk
"A" 200 acres. Calc. carrying capacity 40 (?) or 1 : 5	37 or 1 : 5.4 (1929–30)	1 or 2.7%. Av. 92 days	Mm heavy + Dm ? Ct heavy + SB mod.	Daily visitors: Mink, Weasel. Occasional: Horned Owl, Redtailed Hawk
	67 or 1 : 3 (1930–31)	No more than 8 or 12%. Av. 99 days	Mm light Dm mod. Ct heavy + SB mod.	Daily visitors: Horned Owl, Mink +, Weasel +. Common: Cooper's, Marsh, and Redtailed Hawks. Occasional: House Cat
	70 or 1 : 2.9 (1931–32)	2 or 2.9%. Av. 75 days	Mm light Dm mod. Ct heavy + SB mod.	Daily visitors: Horned Owl, Weasel. Common: Grey Fox, House Cat, Mink. Occasional: Marsh and Redtailed Hawks
	41 or 1 : 4.8 (1932–33)	None for 43 days under obs.	Mm mod. Dm mod. Ct mod. SB mod.	Daily visitors: Horned Owl. Common: Weasel

TABLE II.—*Continued*

Area	Quail density	Rate of predation	Buffer population	Predators present in av. covey territory. + signifies extra heavy density
"B" 200 acres. Calc. carrying capacity, pheasants and quail 77 or 1 : 2.6	Quail 20 or 1 : 10. Pheas. 12 or 1 : 16.7. Combined, 1 : 6.2 (1929–30)	Quail 0. Pheas. ? Av. 80 days	Mm heavy + Dm mod. Ct mod. SB mod.	Daily visitors: House Cat, Weasel. Common: Redtailed Hawk, Mink
	Quail 47 or 1 : 4.2. Pheas. 30 or 1 : 6.7. Combined, 1 : 2.6 (1930–31)	Quail 0. Pheas. ? Av. 70 days	Mm mod. Dm mod. Ct mod. SB mod.	Daily visitors: Redtailed Hawk. Common: Marsh Hawk, House Cat, Weasel
	Quail 26 or 1 : 7.7. Pheas. 50 or 1 : 4. Combined, 1 : 2.6 (1931–32)	Quail 0. Pheas. 3 plus. Av. 70 days	Mm ? Dm mod. Ct heavy SB mod.	Daily visitors: Redtailed Hawk +. Common: House Cat, Mink, Weasel
Des M. Wtrwks. 1400 acres. Calc. carrying capacity 168 or 1 : 8.3	180 or 1 : 7.8 (1932–33)	About 12 or 6.8% (?). Av. 95 days	Mm heavy Dm heavy Ct heavy + SB heavy +	Daily visitors: Redtailed and Redshouldered Hawks. Common: Cooper's Hawks. Occasional: Horned Owl
L. St. Pk. 500 acres. Calc. c.c. 44 or 1 : 11.4	52 or 1 : 9.6 (1932–33)	About 6 or 11.5% (?). Av. 96 days	Mm mod. Dm mod. Ct mod. SB mod.	Daily visitors: Barred Owl, Redtailed and Cooper's + Hawks, Red Fox, Mink. Occasional: Horned Owl
Ames 1500 acres. Calc. c.c. 147 or 1 : 10.2	177 or 1 : 8.5 (1932–33)	12 or 6.8%. Av. 95 days	Mm mod. Dm mod. Ct light SB mod.	Daily visitors: Red Fox, House Cat. Common: Horned Owl, Redtailed, Marsh and Cooper's Hawks, Mink
Ft. Des M. 640 acres. Est. c.c. 320 or 1 : 2	116 or 1 : 5.5 (1932–33)	About 7 or 6% (?) (Calc.). Av. 80 days	Mm mod. Dm mod. Ct heavy SB mod.	Daily visitors: Horned Owl, Redtailed and Marsh Hawks, Red Fox. Common: Barred Owl, House Cat, Mink, Weasel

over the data, a brief resume of some of the area findings may be convenient.

From December 1st to February 16, 1929–30, area "G" lost through predation about 6 out of 121 or 5 per cent; December 22 to March 15, 1930–31, 13 of 257 or 5 per cent; December 1 to March 20, 1931–32, about 61 of 400 or 15.3 per cent; for an average winter period of 106 days, 1932–33, 61 of 406 or 15 per cent. No increase in predation rate was shown as the population in a quail per 10 acres environment rose from a bird per 26.4 acres to one per 12.5; when the density became top-heavy at around 400 birds or one per 8 acres the predation rate mounted swiftly and remained constant, at least for the last two seasons. An increasing density of grey foxes (*Urocyon cinereoargenteus*) appeared not significantly related to the increased quail mortality (Errington, '33f).

That the rate of predation is not contingent upon quail density as such, but upon the density in relation to environmental carrying capacity is borne out by the data from other observational areas.

For area "C" representing poor environment (calculated carrying capacity, one bird per 64 acres), the 1929–30 winter loss from predators was placed at 25 per cent of a sparse though top-heavy population of a bird per 40 acres; in 1930–31, but 5 per cent of a bird per 61 acres population. Area "H," in 1931–32, with a much higher quail density (1 : 4.4) but with an intrinsically high carrying capacity, lost around 5.5 per cent from predation. The population of "E" (estimated carrying capacity approximately equal to that of "H" or 1 : 2) suffered no known loss from predation alone, although a Red-tailed Hawk preyed upon a doomed, starving covey. The 1930–31 density of 1 : 21.8 lost one bird or 2.3 per cent; the 1 : 12.3 density for 1931–32, also a bird or 1.3 per cent. Illustrative of the lightness of predation upon a moderately heavy but securely situated Iowa population (1 : 5.5 density in an estimated 1 : 2 environment), the birds of the 1932–33 Ft. Des Moines observational area lost, according to fairly good evidence, in the vicinity of 6 per cent or less.

The ascending scale of predator pressure coincident with quail density increase past carrying capacity is portrayed by the interchangeable use of data from the two similar areas, "D" and "F." The standardized data from table I, and as expressed graphically in fig. 1, give no predation loss for the area "D–F" environment when 78 per cent stocked with bob-white, but this figure is weak because of the shortness of the observational period. For the environment completely stocked up to carrying capacity (1 : 20) the winter predation rate was 2.9 per cent per 90 days. A population calculated to have over-stocked the environment by 12 per cent lost at a rate no less than 4 per cent. From here on the predation losses rose disproportionately, a 19 per cent over-population losing at the rate of 13.3 per cent; a 69 per cent over-population, about 21.4 per cent; a 97 per cent over-population, 24.4 per cent.

Data from specific territories point the same direction as those from the

larger areas. Territories evidently not filled up to carrying capacity afforded normally excellent protection to winter-resident bob-white. Ordinarily, small coveys stationed in territories capable of accommodating many more birds may be expected to winter with trivial if any predation loss; some territories, in fact, were so strong as to render substantial populations literally immune from native enemies, winter after winter.

Territorial adequacy for wintering quail grades off into territories so poor that birds cannot survive in them at all. One such territory in area " G " has been observed for four seasons. The first winter, 8 birds were early residents but promptly moved out. The territory was not occupied the following season. Almost complete annihilation atttended the 1931–32 attempt of a covey of 26 to maintain itself (Errington, '33c, p. 25, group XXXII), and the last season's notes revealed the failure of a covey of 12.

Occupancy of a lethal territory as well as of others distinctly inferior in quality follows as a natural consequence of over-crowding. Data on four territories used by quail but one winter and then only as a response to necessity give uniformly heavy loss rates; losses from miscellaneous causes, principally predation, ran from 37 per cent to 77 per cent with an average loss rate of 57 per cent per 90 days.

The area " G " data, I think, exemplify quite typically the history of mid-west quail populations. The deep snows of 1928–29 left a starved population remnant far below the normal carrying capacity of the land. The following moderately severe winter 1929–30, the low quail density situated in intrinsically strong environment survived in excellent shape. The winter of 1930–31 was mild and open, and the quail density, while rising, was still sufficiently low to be easily accommodated by existing first-class environments, with but little more than nominal losses.

However, the better coverts were inadequate to take care of the 1931–32 and the 1932–33 populations, and the overflow tended to fill territories of decreasing desirability, this being marked by a pronounced acceleration of predation. Eviction of certain coveys by the clearing of roadside and fencerow brushy vegetation, the burning of strategically located brush piles, and the removal or destruction of essential food sources was seemingly counterbalanced by other man-made changes inadvertently productive of additional territories.

Predator Species and their Population Densities in Relation to Depredations upon Bob-White

In an analytical treatment of the rôle of the predator factor in the life-equation of the bob-white, the question of predator and buffer species and their densities should receive attention. The data submitted in table II may provide a partial answer.

Within ordinary limits, the kinds and numbers either of predators or of buffers do not appear to have appreciable effect on north-central bob-white

winter predation loss rates. Extreme cases showing exceptions to this generalization could doubtless be cited, but this discussion is concerned less with extremes and more with what can be called commonplace population phenomena.

Innumerable probabilities of error confront attempts to express variable or unmeasured or unmeasurable factors as constant values; even so, some idea of the relative abundance of predators and prey may be conveyed.

Buffer populations—meadow mice (*Microtus*), deer mice (*Peromyscus*), cottontail rabbits (*Sylvilagus*), small birds and other winter-active vertebrates comprising staple foods for flesh-eaters collectively—were not estimated in accordance with any technique approximating census methods. Admittedly not all to be desired from the sandpoint of accuracy, the designation of the status of populations as heavy, moderate, or light (table II), may not lack usefulness. For instance, meadow mice reached a high cyclic peak in south central Wisconsin, 1929–30, and for the next two years were down so low that one saw little sign of them at all; there is slight likelihood for mistake when species population levels are as distinctly in contrast as this.

With respect to predator populations, it has been possible to arrive at fairly definite figures for certain species, notably resident owls and those hawks exhibiting preference for given perching trees, through the locating of roosting and nesting territories. Track and den studies gave the best criteria for the calculation of mammalian predator numbers. Small owls, hawk species not known even to molest adult quail, raccoons (*Procyon*), dogs and slow mustelines as skunks (*Mephitis*) and badgers (*Taxidea*), and other lesser predators are neglected in the data tabulations.

Predator densities as such, even if known, may or may not be of material aid in analyses of quail environments. They may actually be misleading, for it is entirely within reason that covey territories may be situated in parts of an area little frequented by predators, though predator densities for the area as a whole may be high. In an attempt, then, to present a more correct picture of potential exposure of quail to predation, the predator densities of table II are indicated on the basis of how often specific predators may be expected to occur in usual covey ranges. It is not, of course, flawlessly accurate, to state, as in the tabular data, that a predator species is a daily visitor or a common or occasional visitor, but by so doing we may get something of a background for comparisons.

Although table II summarizes the quail-buffer-predator data in possession and substantiates the thesis that if the environment is not adequate something will befall the vulnerable excess quail population anyway, the inference is not to be made that the predatory species listed are on a plane of equality as quail enemies.

Barred owls (*Strix varia*), house cats, minks, and weasels were not detected preying upon winter bob-white at all (see Errington, '32b; '33c; '33d). High densities of foxes (*Vulpes* and *Urocyon*), marsh hawks, and red-tailed

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hawks may correspond to high quail mortalities, but this may not mean much; it so happens that only occasional losses in the observational areas could be charged to them, particularly to red-tails for which species I have never been able to record the taking of quail in good physical condition.

Great horned owls and Cooper's hawks, especially the former, have been responsible for the bulk of the quail mortality traced to specific predators, but it is certainly difficult significantly to correlate material winter predation rates (over 5 or 6 per cent) with the presence and frequency of these two species. Wide fluctuations in numbers of the two, down to complete absence of both, did not result in any noticeable changes in net predation rates upon vulnerable populations. And adult bob-whites entrenched at secure population levels in a strong environment were neither very convenient nor very available even to such formidable predators as great horned owls and Cooper's hawks.

I am, therefore, inclined toward the perhaps heretical thesis that predaceous man, with his improved firearms and equipment, trained dogs, and his habit of pursuing prized game species, may be the one predatory enemy of quail capable of reducing solely by direct attack their numbers much below the carrying capacity of the land. Goshawks might conceivably, during their infrequent invasions from the northern wilderness, prey severely upon bob-white populations practically invulnerable to less efficient native enemies.

Rate of Increase of Bob-White Populations in Relation to Environmental Carrying Capacity

From a consideration of very limited data, the rate at which a bob-white population recovers numerically during a given breeding season appears governed principally by the density of the breeding stock in relation to the carrying capacity of the environment. Populations of low densities in environments strongly favorable displayed high rates of increase, whereas for populations nearer carrying capacity the rates became progressively less.

This is especially well brought out by the data from area " G," an area of sufficient size (5 square miles) to give reliable figures.

Subsequent to the drastic reduction of the severe winter of 1928–29, the population had risen from an undetermined low density to a bird per 26.4 acres by January 1, 1930; by January 1, 1931, the density was a bird per 12.9 acres, a net increase of 112.2 per cent; by January 1, 1932, a bird per 8 acres, a further net increase of 55.6 per cent; by January 1, 1933, a bird per 7.9 acres or a net increase of but 1.5 per cent. The population has now reached what may be regarded as an approximate equilibrium, subject, however, to variations in environmental pressure either of ordinary or of extraordinary weight.

The area showed from April to December 22, 1930, an increase of 129 per cent, or a rise from a bird per 28.5 acres seed stock to a population of one per 12.5. Early December censuses, 1931, gave a 69 per cent increase, or a rise

from a bird per 13.6 acres April seed stock to a one per 8 acres population. The rise for 1932 was 40 per cent from seed stock, or from a bird per 11 acres in April to one per 7.9 by December.

It is doubtful if rate of increase figures from the smaller areas—because of the certainty of movement in and out during the summer months—are at all reliable but some will be cited to show the trend of the evidence. It has already been mentioned that, where seed stock populations have not actually been counted through March, careful computations have been made on a pro-rata basis.

Next in reliability to those for area " G " are the data from " E " (1½ sq. mi.). From an April 1930 seed stock of a bird per 80 acres, the area showed by mid-December an increase of 267 per cent or a rise to a bird per 21.8 acres. The following breeding season, the rise was from a bird per 29 acres to one per 12.3, or 136 per cent increase from seed stock.

At one extreme we may find well situated remnants of substantial populations recovering from cataclysms at a not far from unimpeded rate, an imperfect illustration of which may be obtained from the 1932 experience with area " H." The population had been depleted to a bird per 26.7 acres by a late winter storm, although the intrinsic environmental carrying capacity was estimated at around a bird per 2 acres. A hasty survey the next winter, without actual census work, left the impression that there were virtually as many quail and in about the same places as before, or a density between a bird per 4 and 5 acres.

Assuming a complete population recovery from seed stock for " H," the rate of increase would approach 500 per cent. The complete recovery of the population in one season is entirely plausible, but not independently of the influx of outside birds. In probability the actual increase from seed stock amounted to something like 300 per cent or six young per pair.

One bird raised per pair represents a common increase rate for bird per 10 or 12 acre populations that have reached carrying capacity. This would approximate Kendeigh's ('33) calculated annual surplus of 39 per cent for bird per 10.9 acre populations, a figure applying to average Ohio environment but one comparable to the 40 per cent for the not dissimilar 1932 peak density of area " G " in Wisconsin.

I would suspect that the apparent connection between the adequacy of the Wisconsin quail breeding and wintering ranges is not so much a matter of nesting grounds as it is of fall territories for the season's juveniles. The 1933 Iowa field studies (unpublished) have brought out evidence of a heavy November wave of mortality coincident with the shrinkage of cover due to the dropping of leaves from deciduous vegetation. Wisconsin experience also shows the first snowfalls are correlated with conspicuous predation.

Even where a large proportion of the nesting attempts end in failure, the propensity of the quail to renest again and again until successful or until the

breeding season is over (Stoddard, '31; Errington, '33e) may likely produce more birds than a weak fall as well as a weak winter range can effectually accommodate. The theoretical possibility exists, then, that comparatively good or bad hatches may have decidedly less influence upon bob-white population levels than the receptivity of the environment for grown birds. Whether things work out this way I do not pretend to know.

Discussion

This paper is written primarily as a presentation of data. I am not at all positive that I know their meaning, nor have I any awareness of drawing conclusions past those substantiated by the evidence. Table II constitutes, in condensed form, practically all that I possess on the subjects treated which I deem worth publishing, irrespective of agreement or discrepancy with any prior theses I may have advanced. If subsequent researches or more reasonable interpretations render present conclusions untenable, well and good.

Further, let it be emphasized that this paper is not intended as a hard and fast proof of anything. The data are merely submitted for their informational value and for whatever legitimate use they may have for scientists, wild life administrators, and the conservation-minded public.

As a working basis for wild life management we may have something a little more substantial or a little less futile than sundry dogmas in general circulation. It will do no harm to recognize that as long as there are quail in excess of environmental carrying capacity they cannot be expected to maintain themselves at that level; that as the weight of one inimical factor is diminished the weights of others on a vulnerable population may compensate. Insecure surplusses seem to be reduced, be the environments good or poor. Logical management should strive to keep environmental carrying capacity well ahead of population until the optimum density is attained. Bob-white management, to be effective, then, means largely the intelligent manipulation of food, cover, covey territory, and man.

Summary

1. Winter survival of bob-white populations under observation appeared—save when over-shot, starved out, or decimated by natural cataclysms—largely determined by the carrying capacity of the land, as expressed in terms of coverts habitable for given population levels of birds.

2. Kinds and numbers of wild predators, migrant or resident, had no measurable influence on carrying capacity, despite heavy quail mortality sometimes due to predation. Material winter losses from predators have pointed to quail populations top-heavy for the environment. Stated otherwise, the predators consumed mainly an ill-situated surplus. Material predation upon bob-white was rather a symptom of species vulnerability than a factor responsible for or even importantly contributory to the low or precarious population densities frequently encountered in mid-west quail range.

3. The *absolute* quail density did not have the close correlation with the rate of winter predation as did *comparative* density. The density of the population in relation to the carrying capacity of the environment, high or low, was of fundamental significance.

4. The rate of bob-white population recovery during the breeding season was seemingly conditioned by the degree to which the habitable fall and winter environment was filled up. Progressive increase of environmental resistance was manifest in cases where populations ascended toward levels less and less easily accommodated.

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THE ORGANIZATION OF THE CREOSOTE BUSH WITH RESPECT TO DROUGHT

ERNEST H. RUNYON

University of Cincinnati

The creosote bush, *Larrea tridentata* Cav.,[1] is the most widely distributed, ubiquitous and successful perennial plant in the southern desert regions of North America. Its range extends from southern California to central Texas and southward into lower California, and the arid plateau of northern and central Mexico, a domain over which it is one of the most abundant elements of the vegetation. Its habitat differs greatly in the most widely separated parts of its range. In spite of an evergreen habit the shrub is renowned for its ability to survive long periods of drought accompanied by high temperature and low atmospheric humidity.

The commanding position of *Larrea* in American desert vegetation and its extreme xerophytism have led Dr. Forrest Shreve to organize a group of investigations on its water relations and habitat requirements as one of the projects of the Desert Laboratory of the Carnegie Institution of Washington, at Tucson, Arizona. The writer has been engaged in an investigation of the foliar water of *Larrea,* and the results of this work are now in preparation for publication. The present paper embodies certain general observations on the reactions of the shrub to various water conditions. The field work was done at the Desert Laboratory, and the writer wishes to express here his indebtedness to the Carnegie Institution for the facilities which have been placed at his disposal.

The distribution and ecological features of *Larrea* have been described by Shantz and Piemeisel ('24) and by Shreve ('31), and earlier references have been cited by the latter author. Spalding ('04 and '09) has described the tolerance of the shrub to calcareous hardpan (caliche). Cannon ('05 and '18) has shown its intolerance of poorly aerated soil and has described its extensive root system, as well as the influence of water supply and temperature on growth and transpiration.

In spite of the position of *Larrea* as a dominant desert plant, its foliage shows no extreme xeromorphic features. As may be seen in figures 1, 2 and 3, the leaves are small (often less than 70 sq. mm.) but are produced in prodigious numbers. At no time are the bushes entirely defoliated, as are so many of its companion species. A distinctive character of its foliage is

[1] Zygophyllaceae. Synonyms: *Covillea tridentata* (DC.) Vail, *Neoschroetera tridentata* (DC) Briq., *Covillea glutinosa* (Engelm.) Rydb.

its coating of resinous substance, whose pleasant aroma gives this plant its popular name, creosote bush. The rôle of this substance will be considered later. Another feature of the leaves is the movement of their parts, the two divisions of the leaf being ordinarily considered to be the two leaflets of a

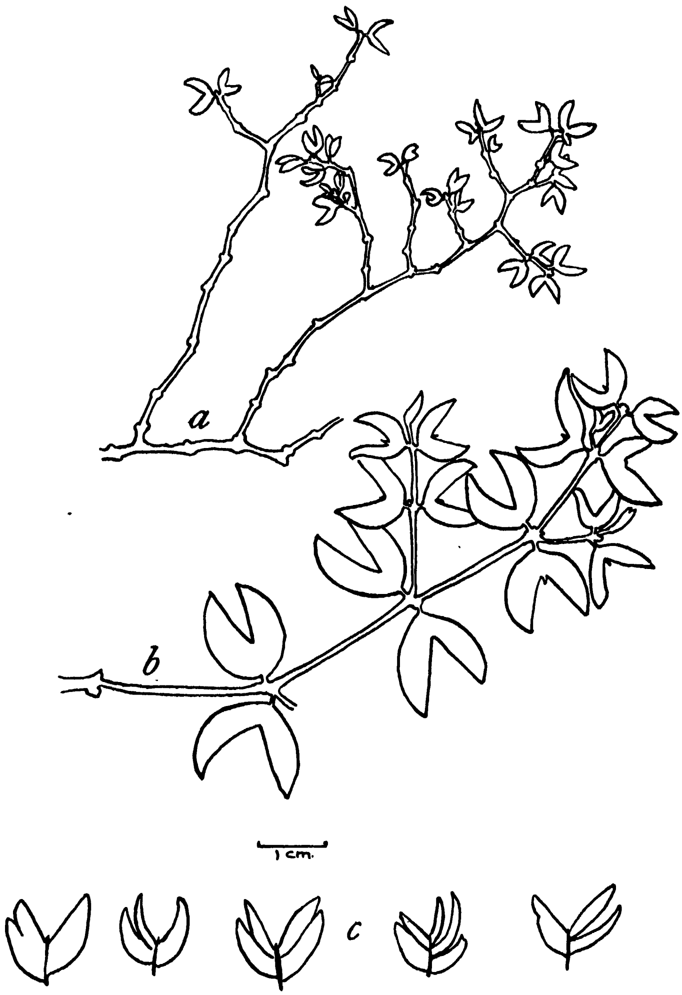

FIG. 1. Foliage of *Larrea,* traced from blue prints. *a,* twig and leaves from a bush in dry soil. *b,* twig and leaves from a bush well supplied with water. *c,* leaves showing a tendency towards a multifoliolate condition.

bifoliolate leaf. These leaflets close upwards towards each other under various conditions; but as this movement is predominantly nyctinastic in nature, it provides but little protection in the way of reducing transpiring surface. The statements of Ashby ('32) that *Larrea* leaves ". . . in dry weather are sometimes stuck together along their adaxial faces." and that " The inclination

of the leaves to one another seems to depend upon the amount of rain, or the water content of the soil." are not confirmed by the writer's observations of the creosote bush made during the dry seasons of four consecutive summers (1928–1931) in the Tucson region. The only leaves whose adaxial faces adhere generally, are immature ones which have never opened. These, if anything, are more abundant on well watered bushes than on poorly watered ones. The " leaves " do not incline towards each other; and the inclination of the pinnae towards each other has no conspicuous relation to the water supply except in this respect: that whereas the leaflets of favorably situated

Fig. 2. Effect of water conditions on leaf size and number. Right, a shoot from a dry-soil bush; note the small leaves and irregular branching. Left, a shoot from an artificially irrigated bush; note the abundance of leaves, and symmetrically alternate branching.

bushes show a marked diurnal movement (closing upward at sunset, and beginning to open gradually about midnight, with minor movements during the day), the leaves of dry soil bushes are *permanently open,* there being insufficient diurnal change in water content to permit the movements. It is true that the pinnae of leaves undergoing a shortage of water are likely to be somewhat more inclined toward each other than the pinnae of other leaves; but anything short of almost complete closure could be of no appreciable protection from the blistering sun and desiccated air that *Larrea* must withstand.

The internal structure of the leaves gives but little clue to the understanding of the remarkable resistance of the creosote bush to drought. Figure 4 shows in outline the cellular structure of two leaves as seen in transverse section. These leaves happen to be from bushes in comparatively favorable water conditions, but leaves from bushes in dry soil show the same anatomy. Aside from the absence of spongy tissue, the leaf could hardly be described

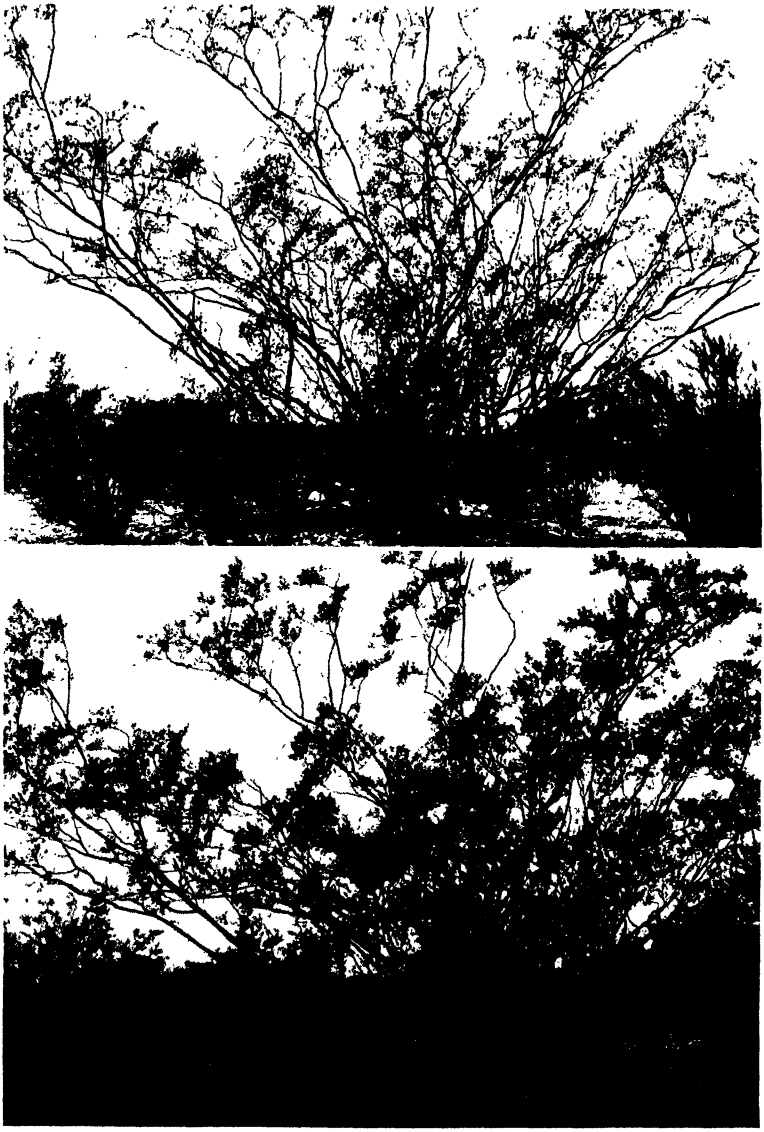

FIG. 3. Effect of water conditions on leaf size and number. Above, a bush in time of drought. Below, the same bush after mid-summer rains, showing difference in density of foliage.

as xeromorphic. It is not at all difficult to find large intercellular spaces; the cuticle is not as thick as might be expected on a desert plant; and stomata, far from being reduced or specially protected are decidedly numerous and mesomorphic (see also Walter, '31 and Ashby, '32), being present in both the

upper and lower epidermis. In short, the extreme xeric character of this plant would not be expected from the structure of the mature leaves.

As has already been indicated, the success of *Larrea* in the desert is remarkable because it is always in leaf. Seasonal changes, however, are conspicuous. Obvious growth is initiated only after a period of rain. If the water supply is abundant, growth is very rapid; leaves—and later, flowers and fruits—are produced in great abundance. If, on the other hand, the water supply is meagre, the growth is slower, and the leaves, flowers and fruits are not only fewer, but also much smaller. The relation of water supply to

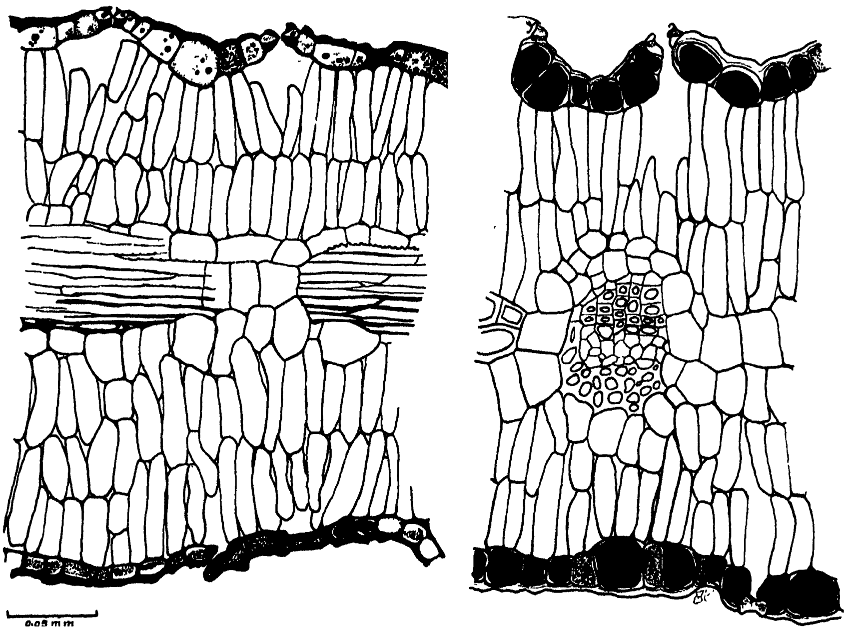

FIG. 4. Transverse sections of portions of two mature *Larrea* leaves. Cell content not shown except for epidermis. Camera lucida drawing.

leaf size and density is shown in figures 2 and 3. On bushes favorably situated with regard to water a variable small proportion of the leaves may be more or less tri- or multifoliolate instead of bifoliolate (fig. 1*c*). These more mesic appearing leaves have never been found on dry-habitat *Larrea*. The luxuriant dark green symmetrical bushes everywhere to be seen where the water supply is favorable, are in striking contrast to the thin, scraggly bushes of the desert. Although confined in its distribution to the most arid parts of the continent, the creosote bush attains its maximum of vegetative vigor only when supplied with abundant water.

Another characteristic which may throw some doubt on the fundamental xeromorphy of this plant may be mentioned in passing. An even less com-

pact chlorenchyma than that figured and described above was found in the case of some leaves of seedlings grown in the greenhouse of the University of Cincinnati. *Larrea* seedlings have simple and linear cotyledons. The leaves at the next two nodes have the regular bifoliolate form. There is thus no external evidence of a juvenile condition which might relate to ancestry, other than the change from simple to compound leaves. However, transverse sections show that instead of the normal isolateral structure shown by the upper leaves of the seedlings, these cotyledons and first leaves have a dorsal spongy layer with irregularly lobed cells more typical of mesophytes. If this may be interpreted as a suggestion of a more mesic ancestry, it falls in line with Spalding's view ('04) based on the general reactions of the bush to abundant water. The properties which adapt *Larrea* leaves to drought conditions are seemingly added to an organization which to a considerable degree is mesomorphic.

The creosote bush is described as an evergreen. But as week after week passes with no rain to alleviate the hot dryness of soil and air, the older leaves gradually yellow and fall a few at a time, and what remain are brownish rather than green. In the very driest seasons only buds and immature leaves remain. At all other times some of the full sized leaves are to be seen adhering to the twigs. The reduction of transpiring surface by leaf abscission seems thus to be incommensurate with the requirements for enduring the extreme drought.

Many twigs also are shed, and under the most extreme conditions, large older branches die, leaving fewer and younger parts to compete for the meagre water supply. Older bushes are almost invariably mulched with an accumulation of these dead branches. Aside from the more favorable balance brought about between the water getting and water spending parts of the plant, there results from the stem shedding an interesting effect on the branching.

Although *Larrea* has opposite leaves, branching under continuously favorable conditions is alternate, *i.e.*, there is developed at each node one and only one branch shoot. After a period of drought, however, with more or less dying and breaking off of stems, followed by a resumption of growth at the return of favorable conditions, there may develop at each node one or two other branches, resulting in an opposite or whorled system, while at other nodes there may be no branch at all. Thus on well watered bushes, especially those not subject to periodical drought, symmetrically alternate branching on all but the oldest parts is constant, whereas on the common desert plant, branching is very irregular, with frequent occurrence of opposite branching. The drier the conditions, the more stem abscission there is, and the more irregular is the branching and contour of the bushes. It is apparent that this is probably not a specific effect of drought conditions; any factor periodically inhibiting growth might bring about the same result. Actually, however, it is the water relations which control this peculiarity of branching (fig. 2).

Careful study of shoots during and after periods of severe drought reveals

two important facts: first, whatever mature leaves remain on the branches during such periods become yellow and fall soon afterwards, *i.e.*, after rain has made possible resumed activity of younger parts; second, immature leaves and buds are retained through the driest seasons in a partially dormant state resuming their activity when conditions are again favorable. From these facts it is at once evident why mature leaves of *Larrea* show no very marked xeromorphism. They are not included in that part of the plant which endures the more severe drought. It is evident furthermore why the mature leaves of *Larrea* from dry and moist soils show an internal structure which is almost identical; in both cases the leaves have been developed during a time of favorable water conditions, and in neither case are the leaves possessed of any great capacity of drought endurance. In the case of the bush in dry soil, the leaves appear hard and brownish, and whatever degree of vitality they possess is soon lost, for they are shed at the return of favorable conditions, if not sooner. The partially grown leaves and the buds are the truly drought enduring parts of the foliage.

The immature leaves have exactly the same appearance as the mature ones except for their small size,—about half that of mature leaves on the same bush. They exhibit a resistance and dormancy in their arrested state of development somewhat comparable to that of seed embryos, but unlike the seeds, with no obvious protection from the extreme conditions to which they are exposed. The buds are likewise unprotected, there being no bud scales. Hard, dry appearing, and brownish, the leaves are nevertheless alive, and capable of renewed growth when conditions are again favorable. They do not show the

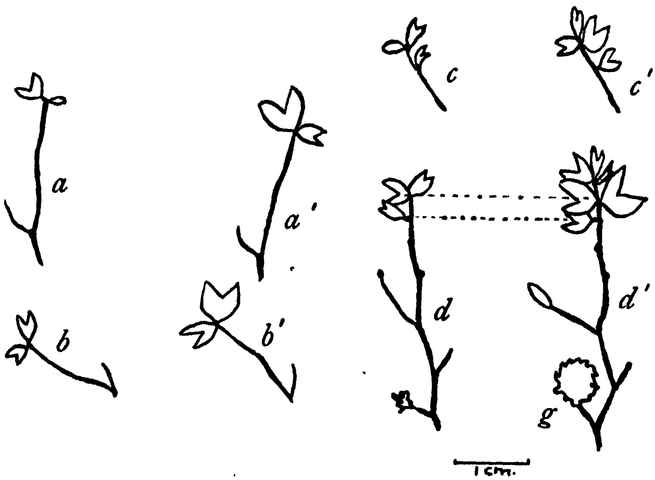

FIG. 5. Revival of dormant leaves after drought. (From blue prints.) Four twigs (*a*, *b*, *c*, and *d*) with their dormant, partially developed leaves and naked buds. The same twigs (*a'*, *b'*, *c'* and *d'*) after return of favorable conditions, showing resumed growth of the leaves and buds (*g*, gall). (Other leaves present on the twigs were shed or did not show further growth, and were omitted from this figure for sake of clarity.)

leaflet movements shown by leaves of well watered bushes; their water deficit is very high, their transpiration is very low. At the return of rain—it may be after several months—some of these miniature leaves resume growth. This is shown conclusively by inspection of blue prints of intact shoots made before and after a period of watering (fig. 5). Some of the smaller leaves enlarge, often to full size; other leaves remain in their stunted condition, although they may become active as judged by their increase in water content and resumed leaflet movements. A very few seed plants and many of the lower plants withstand a period of drought by becoming air-dry; their dormancy is complete. The creosote bush is to be contrasted with these, for water content studies (to be reported in detail later) show *Larrea's* dry season leaves to have a water content of 40–50 per cent of their dry weight, and a slight diurnal fluctuation of water content. These leaves are therefore resistant to drought in a condition which can not be described as complete dormancy. No other case is known of leaves which may undergo a cessation of development just before maturity, survive such a period of extreme drought, and then resume growth.

Walter ('31) reports that the leaf thickness is the same for bushes of contrasting water conditions, and challenges the remarkable statement of Schratz ('31) that Larrea leaves may undergo a volume decrease to about one-fourth the original volume. Only slight volume changes have been found by the writer, and it is to be emphasized that the leaves which should be compared are not only the mature leaves of different bushes, but the young and older leaves of the same bush. The young leaves which have the drought endurance capacity are smaller in every dimension. Figure 6 shows the cross section of a portion of a leaf which has not yet opened. Insufficient examination has been made of the structure of these partially grown leaves, but from the one shown it is evident that the cell arrangement and number is practically the same as in the mature leaf. The difference is in cell size. The change from resistance to non-resistance in the case of these leaves, as for many organisms, involves among other things an intake of water, vacuolation of the cytoplasm, and incidentally, an increase in cell size.

The resinous material, referred to previously, is particularly prominent on young leaves (fig. 6*r*). No experimental data have been reported in the literature relating to the significance of this substance in the water economy of the plant, nor, in fact, any definite information regarding its chemical nature. It is variously referred to as resin, varnish, shellac, wax, mucilage, etc., and is usually, without evidence, credited with the function of reducing transpiration (Volkens, '90, Wilson, '93, Spalding, '09, Shantz and Piemeisel, '24, Carlock, '32). Ashby ('32) found no evidence that the stomata are clogged; and those who have measured the transpiration of moist bushes having leaves sticky with this substance have not found their water loss particularly low; indeed the transpiration rate of such leaves is unexpectedly high (Spalding, '04, Schratz, '31, Ashby, '32).

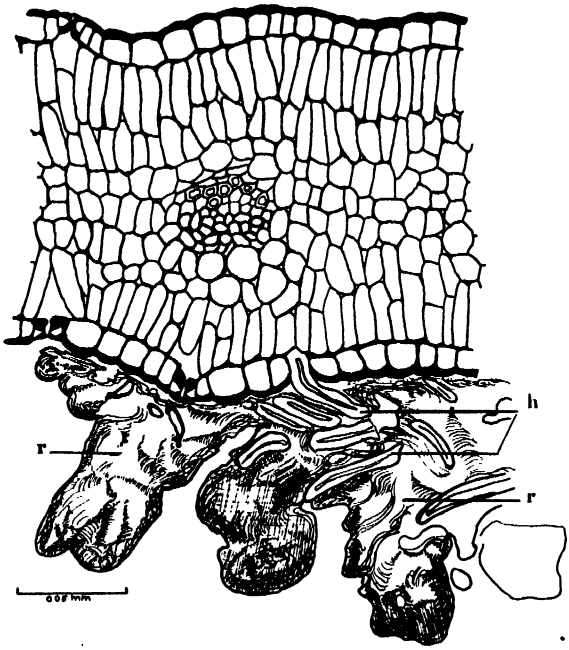

FIG. 6. Transverse section of a portion of a leaf still in bud. *r*, resin; *h*, leaf hairs. Camera drawing.

This aromatic substance is sticky on fresh new growth, and yellowish brown in color as seen by stains left on fingers and by microscopic examination. It is soluble in alcohol, but not appreciably so in water. It becomes less sticky, more insoluble, and gradually indurated as the leaves or twigs become older. It undoubtedly belongs to that group of substances, ill defined chemically, known as resins. In microscopic preparations it is seen adhering to the epidermis and leaf hairs in irregular masses (fig. 6). In some leaf sections, as of those in figure 3, a substance of appearance very similar to the external material occurs *within* the epidermal cells, more or less completely filling the lumen. In the process of making paraffin sections more or less of the external substance is removed by solution or otherwise. The intracellular substance stains darkly with haematoxylin or methylene blue, and is sometimes in globules rather than in one solid mass, possibly due to partial dissolution in the fixing or staining fluids. When sections are treated with concentrated sulphuric acid the intracellular substance is seen in the form of cubical or tabular masses which float free from the dissolving tissues. The majority, or in some cases nearly all of the epidermal cells exclusive of the guard cells of some leaves may be filled with this amber brown substance, while the epidermis of other leaves may be nearly or quite free of it, the external material being present, however, overlying these cells.

It has not been demonstrated that these substances play an important rôle in the water economy of this plant, however probable this may seem. Stomatal clogging or covering does occur, as may be seen in figure 6; no doubt this is of more common occurrence on the partially developed drought enduring leaves than on fully expanded ones.[2] Whether stomata are clogged or not, it is unquestionable that cuticular transpiration is checked by these water-insoluble materials overlying and in the epidermis. When these substances become hardened, as they soon do, it is possible that they may act mechanically in preventing wilting. *Larrea* leaves do not wilt. The solid material inside of the epidermal cells, by maintaining rigid form in spite of the tendency of the cells to contract due to water loss, may prevent the injury usually resulting from drying.

Summary

1. The creosote bush, the most successful and conspicuous xerophyte in the desert regions of North America, thrives on abundant water.
2. The reactions to changes in the water supply involve striking changes in the density and color of the foliage, and a peculiar difference in branching.
3. The leaves are distinguished by no extreme xeromorphism, and yet they are in part persistent throughout the driest seasons.
4. Leaves of plants in dry and in moist soil have the same structure.
5. Leaves which successfully endure the most prolonged and severe drought are only partially grown.
6. The dormancy of these leaves is not complete; they show the unique ability of resuming growth and activity after return of favorable conditions.
7. One factor in the drought resistance of *Larrea* leaves may be the hardening of resinous substances which occur on and within the epidermal cells.

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[2] Unfortunately, sufficient material has not been examined to make certain this point. Ashby's evidence that stomata are not blocked was that imprints of the stomata were always obtained in cellodion films formed on the leaf surface. However, it may be that the resin comes off with the cellodion when the latter is stripped from the leaf.

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BODY TEMPERATURE OF FRESH WATER FISHES [1]

Ralph G. Clausen

N. Y. State College for Teachers, Albany, N. Y.

A thermoregulatory mechanism in cold-blooded animals has been the object of a long diligent search. For, although a cold-blooded animal is one whose body temperature varies with the temperature of the surrounding medium, it is difficult to conceive of a living body so nicely attuned to its environment that the energy produced by the basal activities is expended without any increase in the temperature of the animal body. The relative ease with which one can apprehend absolute poikilothermism in a sessile animal is contrasted by the difficulty of imagining the same condition in an animal as active as a fish. Perhaps this is why there has been so much interest in the relationship between the body temperature of fishes and the temperature of the surrounding water (Carter, '87, Kidder, '79, Simpson, '07, Loeb, '12, Wells, '14, Belding, '28).

The previous attempts to determine the difference between the temperature of the surrounding medium and the temperature of the fish's body present absolutely no uniformity of results. In a table compiled by Rogers ('27, p. 353), the results of several investigators show that the body temperature of a fish may vary between 9.3°F. above (Broussonet) and 2.8°F. below (Davy) the temperature of the water. It is significant that in this table most of the experiments show that the temperature of the fish is higher than the temperature of the surrounding medium. Rogers, who with Lewis ('14) showed that the temperature of an earthworm was the same as the temperature of the surrounding medium, states that from work he has done on fishes he reaches the same conclusions. However, he publishes no data to support this conclusion.

Apparatus for the Determination of Body Temperature

In order to maintain any constancy in the readings of the thermometer, it is essential that the apparatus cause as small amount of inconvenience to the fish as possible. It is obvious that any attempt to introduce the bulb of a mercury thermometer into the body of the fish would initiate activity on the part of the fish, which might change the temperature of the body. Also the apparatus should be such that it can be left in the body of the fish for extended periods of time in order to check the results.

The apparatus used in these experiments consisted of a copper-constantan

[1] Contribution from the Zoological Laboratory of the University of Illinois, No. 444.

thermocouple and a galvanometer. It was a modification of the apparatus described by Robinson ('27) and similar to that used by Rogers and Lewis ('14) in their work on the earthworm.

The thermocouple was made by soldering the ends of a piece of No. 50 constantan wire alongside two ends of two pieces of No. 50 copper wire. The two free ends of the copper wires led to the galvanometer. All the wires were insulated—the constantan by silk, the copper by cotton—and were dipped in shellac. After the shellac had dried, one of the copper wires was twisted around the constantan wire until the second junction of copper and constantan was reached. The wires were covered by a thick lacquer or a solution of cellu-

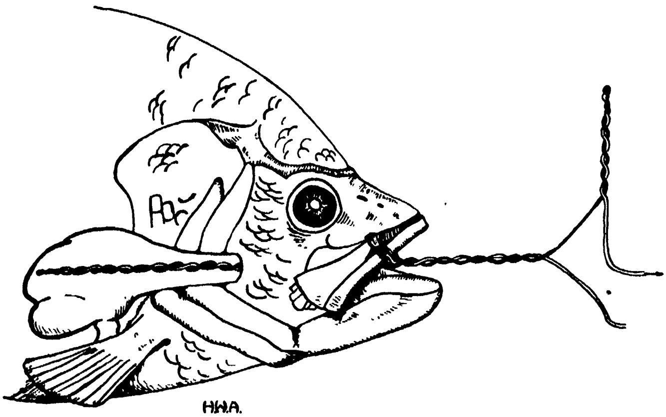

FIG. 1. Diagram of a fish with the thermocouple in its stomach.

loid and acetone. This procedure was not only effective in completely insulating the wires, but made them stiff enough to be introduced into the body of the fish with ease.

The galvanometer was of the moving coil, reflecting type. It was read through a telescope. The distance between the scale and the mirror was so adjusted that each unit on the scale (1 mm.) represented 0.04° C. With practice, each unit could be divided into quarters, so that it was possible to read the differences in temperature to 0.01°C. These readings are not accurate to one one-hundredth of a degree, however, because it was impossible to maintain the water in which the fish was swimming at an absolutely uniform temperature.

Each thermocouple was tested both before and after each experiment. The test consisted of two parts. First, both junctions were submerged in water which had been thoroughly stirred. Second, each junction was placed in water, the temperature of which differed from the water around the other junction by a known amount. The temperature of the water was measured by thermometers graduated in 0.1° C. In this way it was possible to test for short circuits, and also to determine the standard deflection of the galvanometer for the experiment.

Procedure for the Determination of Body Temperature

Whenever possible the fish was placed in the experimental body of water at least twenty-four hours before the thermocouple was introduced. After the fish had become accustomed to its environs, the lacquer-covered junction of the thermocouple was passed through the mouth of the fish into its stomach. The other junction was placed outside the mouth of the fish. The entire thermocouple was held in place by a thread which passed around the maxilla of the fish and was tied to the wires of the thermocouple (figure 1).

After the first few minutes there was no sign of discomfort on the part of the fish. Certainly no great injury was done because some of the fishes have had the thermocouples in their stomachs for over a month with no visible ill effects.

Of course the more active fishes became tangled in the wires if these were not kept out of the way. By floating the wires in a cork, and allowing only enough wire to permit comfortable freedom, most of this trouble was eliminated.

The Fishes Used in the Experiments

Inasmuch as there has been such a wide diversity of results from the work on body temperatures of fishes, it seemed advisable to experiment on divers fishes. The fishes tested in this series of experiments were: Bowfin (*Amia calva* L.), Carp (*Cyprinus carpio* L.), Common sucker (*Catostomus commersoni* (Lacepede)), Channel cat (*Ictalurus punctatus* (Raf.)), Black bullhead (*Ameiurus melas* (Raf.)), Black crappie (*Pomoxus sparoides* (Lacepede)), White crappie (*Pomoxus annularis* Raf.), Blue gill (*Lepomis pallidus* (Mitchill)), Yellow perch (*Perca flavescens* (Mitchill)), Warmouth Bass (*Chaenobryttus gulosus* (Cuvier & Valenciennes)).

This selection affords a wide range of habitat differences and phylogenetic distances. It includes fishes which are known to feed during the winter, and others which take almost no food during the winter months. Some of them are more active in the daylight hours, others confine their activity to the dark. There is a representative of the ganoids as well as representatives from the highly specialized centrarchids. Their body covering varies from the heavy scales of the bowfin to the naked bodies of the catfishes.

The Temperature Used in the Experiment

The temperatures at which the experiments were done varied from 0°C. to 35°C. In one aquarium the water was held at a relatively constant temperature, usually at 20°C. or at 25°C. over long periods of time. Another aquarium was sunk in the ground and the temperature of the water fluctuated with the temperature of the air.

Results

The uniformity of the results obtained in these experiments is a direct contrast to the diversity of those gathered by most of the previous workers on this problem. Tables I, II, and III are representative of the data which were obtained in almost every case. The very slight variations from the zero of the galvanometer may easily be accounted for by the changes in temperature of the water which were not registered by the thermometer which was used as the standard.

TABLE I. *Body temperature of Warmouth Bass (Chaenobryttus gulosus) compared with temperature of water. Thermocouple in place 8.IV.32, 8:30 A.M. Fish died 26.V.32*

Date	Hour	Water Temp. °C.	Galvanometer Zero	Galvanometer Reading	Galvanometer Difference	Difference in °C.
9.V.32	3:40 P	18	6.8	6.8	0	0
9.V.32	5:05 P	18	6.9	6.9	0	0
9.V.32	6:15 P	18	6.8	6.8	0	0
10.V.32	8:30 A	18	6.8	6.8	0	0
10.V.32	10:05 A	19	6.9	6.9	0	0
10.V.32	11:10 A	19	6.9	6.9	0	0
10.V.32	4:57 P	19	6.9	6.9	0	0
11.V.32	8:20 A	19	7.0	7.0	0	0
11.V.32	9:25 A	19	7.0	7.0	0	0
11.V.32	3:07 P	19	6.9	6.9	0	0
11.V.32	6:06 P	19	6.9	6.9 [1]	0	0
12.V.32	8:15 A	19	6.8	6.8	0	0
12.V.32	8:50 A	22	6.9	6.7	0.2	0.08
12.V.32	10:00 A	23	6.95	6.87	0.08	0.03
12.V.32	11:15 A	23	6.9	6.75	0.15	0.06
12.V.32	11:40 A	23	6.85	6.85	0	0
12.V.32	4:26 P	23	7.0	7.0	0	0
12.V.32	5:05 P	23	7.05	7.05	0	0
12.V.32	7:30 P	23	6.65	6.65	0	0
12.V.32	8:45 P	23	6.5	6.5	0	0
12.V.32	9:00 P	23	6.6	6.6 [2]	0	0
13.V.32	8:40 A	23	Galvanometer jumping.		No reading	
13.V.32	9:50 A	24	6.8	6.7	0.1	0 04
16.V.32	9:15 A	26	6.8	6.75	0.05	0.02
16.V.32	3:25 P	26	6.45	6.45	0	0
16.V.32	3:45 P	26	6.6	6.62	0.02	0.01
16.V.32	5:00 P	26	6.5	6.5	0	0
17.V.32	10:15 A	26	6.15	6.15	0	0
17.V.32	11:45 A	26	5.95	5.95	0	0
17.V.32	5:00 P	26	5.9	5.9	0	0

[1] Following this reading the fish was stimulated. The galvanometer went to 6.5.
[2] Following this reading the fish was stimulated. The galvanometer went to 5.8.

The temperature of the body of a fish tends to assume the same temperature as the water which is surrounding it. After the fish has become acclimated, and as long as it is quiescent, the body of the fish has the same temperature as the water. These results bear out the statement of Rogers ('27) and coincide with his results on the earthworm (Rogers and Lewis, '14).

It must be appreciated that fishes vary greatly in their threshold of stimulation and that the body temperature is the same as the water only when the

TABLE II. *Body temperature of Common Sucker (Catostomus commersonii) compared with temperature of water*

Date	Hour	Water temp. °C.	Galvanometer Zero	Galvanometer Reading	Galvanometer Difference	Difference in °C.
5.I.32	3:00 P	5.3	3.4	3.4	0	0
5.I.32	5:00 P	5.3	3.9	3.9	0	0
6.I.32	2:20 P	2.6	4.3	4.3	0	0
6.I.32	3:00 P	2.6	4.05	4.05	0	0
6.I.32	6:00 P	2.4	4.2	4.1	0.1	0.04
8.I.32	1:30 P	0.0	3.0	3.15	0.15	0.06
8.I.32	3:00 P	0.0	3.1	3.2	0.1	0.04
8.I.32	5:00 P	0.0	3.2	3.2	0	0
8.I.32	7:15 P	0.0	3.2	3.25	0.05	0.02
8.I.32	9:30 P	0.0	3.3	3.3	0	0

TABLE III. *Body temperature of White Crappie (Pomoxus annularis) compared with temperature of water*

Date	Hour	Water temp. °C.	Galvanometer Zero	Galvanometer Reading	Galvanometer Difference	Difference in °C.
29.XII.31	11:00	7.9	3.55	3.55	0	0
29 XII.31	11:05	7.9	3.55	3.55	0	0
29.XII.31	11:15	7.9	3.6	3.6	0	0
29.XII.31	11:45	7.9	3.6	3.6	0	0
29.XII.31	1:45	7.9	3.6	3.43	0.17	0.07
29.XII.31	2:40	7.9	3.6	3.49	0.11	0.045
29.XII.31	3:45	8.0	3.58	3.58	0	0
29.XII.31	5:45	8.0	3.6	3.6	0	0
29.XII.31	7:45	8.0	3.68	3.68	0	0

fishes are not under stimulation. The perch and the members of the sunfish tribe seem to be the most sensitive of the fishes tested in these experiments. If a shadow passes by the aquarium in which they are kept, the body temperature is increased above that of the water. The photosensitive skin of the catfish may be stimulated by the flashing of a light, and the reaction will be shown by a slight increase in the body temperature.

Although this increase in body temperature causes trouble in the experiments because it is almost impossible to do away with every source of stimulation, it serves as an excellent means for testing the thermocouple and making sure that the apparatus is in good working order. After one has failed to get any deflection of the galvanometer for several hours, he naturally begins to doubt the apparatus. The fish may be stimulated, and if a deflection is produced faith in the recording instrument is restored.

The cause of this increase in body temperature is somewhat of an enigma. It cannot be that simple muscular action produces the energy which is given off as heat because as the fish swims about in the aquarium there is no difference between the temperature of its body and the temperature of the water. On the other hand, the catfish was observed to make no movement when it was stimulated by light, but there was an increase in the body temperature. There is a possibility that the reaction is the result of a nervous stimulation

which is coupled with the activity of a ductless gland, and that the reaction is systematic rather than local. The slow recovery to water temperature seems to point to a general effect.

In the light of these results it is not difficult to understand why the majority of the earlier experimenters on this problem found that, after introducing a thermometer into the body of the fish, its temperature was higher than the temperature of the surrounding water. When the mere passing of a shadow is enough to change the body temperature, surely the manipulations necessary for the forcing of a glass tube into the stomach or rectum are sufficient to produce a " fever."

In two cases, a bowfin and a white crappie, there was a variation which might be significant, but it could not be repeated in any of the other fishes. As the temperature of the water was increased, the temperature of the fishes' bodies followed very closely. But above 18.6°C. for the crappie, and 20.4°C. for the bowfin, the temperature of the fishes' bodies remained lower than that of the water. The crappie died while the temperature of the water was above 18.6°C. The temperature of the water around the bowfin was increased to 23.3°C., and then allowed to decrease. This change was done very slowly, and for six hours the body temperature of the fish remained less than the temperature of the water. As the water temperature decreased to 20.4°C., the temperature of the body of the fish assumed the same temperature as the water. The fish was in very poor condition. The respiration was labored. The sense of balance was affected. However, after a few hours in cool water, the fish appeared relatively normal.

Summary

1. Experiments upon a variety of fishes show that the body temperature of a fish tends to take the same temperature as the surrounding water.

2. Stimulation causes a reaction which increases the body temperature above that of the surrounding medium.

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MOISTURE AND pH STUDIES OF THE SOIL UNDER FOREST TREES

G. M. Shear and W. D. Stewart[1]

University of Illinois

A knowledge of the effect of forest trees grown from artificial plantings, on various factors of the environment is becoming continually more important due to the depletion of the natural supply of our most valuable timber. The data that have been collected are chiefly from reforested areas and very little work has been done on trees planted in prairie regions.

In Illinois the feasibility of growing trees from artificial plantings as windbreaks and for commercial purposes was proved at an early date. In 1871 the University of Illinois started a forest plantation to demonstrate this and it has been added to from time to time since then. Under the supervision of T. J. Burrill ('86) the plantings were made on land that was originally prairie. It was in this forest plantation, locally known as the Forestry, that the work reported herein was done.

Most of the research that has been done to determine soil moisture in forested areas is limited to the upper layers of soil, generally in connection with successional studies. Fuller ('14) during the summer of 1911–12 and Groves ('14) in 1913 determined the available soil moisture to a depth of 25 centimeters under different types of forest in the region of Chicago and found that water was available for shallow rooted plants throughout the summer. Batchelor and Reed ('23) made a study of soil moisture under a walnut grove in California and found that the trees were able to reduce the moisture below the wilting coefficient without apparent injury. Their measurements were made to a depth of seven feet. The trees reduced the moisture content of the soil to that depth.

The effect of forest plantings on the pH of the soil is of great ecological significance. While certain species of trees are found on soils of a fairly characteristic pH, little is known as to the effect of the trees on this reaction.

This work was started in the fall of 1927 and continued through the spring of 1929, with a view to determining the available soil moisture under different kinds of trees at various times of the year. In connection with this the pH of the soil at different depths was also determined.

The authors are indebted to Professor H. L. Shantz for his assistance in directing this study.

[1] Formerly of the Department of Botany, University of Illinois. The senior author is now Assistant Plant Physiologist, Virginia Agricultural Experiment Station; the junior author is Assistant Biochemist, Boyce-Thompson Institute.

MATERIALS AND METHODS

The Forestry is located at Urbana, Illinois, on an area which although originally prairie had been used for pasture and for growing corn for a number of years previous to the planting of the trees. The upper end of the area is ten feet higher than the lower and a tile drainage system was installed in the lower portion, which was too wet for cultivation as it stood. The different species of trees were planted in blocks and cultivated when young but later undergrowth was allowed to develop. At the present time, however, the undergrowth has been cleared away and the area is mowed over each summer.

Five stations were established, one under each of the following species: Green ash, *Fraxinus lanceolata* Borck., white pine, *Pinus strobus* L., silver maple, *Acer saccharinum* L., white oak, *Quercus alba* L., and larch, *Larix decidua* Mill. The first three are located in the lower part of the planting on fairly level ground. The latter two are on the higher portion where they receive better natural drainage. Soil samples, usually down to wet soil, were taken by means of soil tubes. Three samples, one foot apart, were taken for each foot and all samples were taken within three to five feet of the trees. The soil was placed in cans with tightly fitting covers and the percentage of moisture determined by drying the samples to a constant weight in a drying oven. All weighings were made after the soil had reached room temperature. The average weight of the samples was about 400 gms.

Moisture equivalents were determined in quadruplicate for each foot from composite samples. The method used was that of Briggs and McLane ('07). From these results the wilting coefficients were determined indirectly by the formula of Briggs and Shantz ('12).

The Youden pH apparatus was used in making the pH determinations, which were made in duplicate from composite samples.

RAINFALL

During 1927, the fall of which year soil samples were first taken, the total precipitation was 55.64 inches. This amounted to 61 per cent above the average for Urbana, Illinois, which is 34.5 inches. The rainfall was much heavier than normal during the last quarter of the year when active tree growth had ceased, thus causing an accumulation of water in the soil. Although this rainfall had not affected the soil moisture to any appreciable extent as was shown by the soil samples collected November 6, it had a marked influence on the water table the following spring. In 1928 the precipitation totalled 32.96 inches, which was 4 per cent below the average. The average of the first quarter of 1929 was practically the same as for 1928 but during April and May it was twice the normal amount. The distribution of rainfall during the period while data were being collected is shown in table I.

TABLE I. *Monthly rainfall covering period of sampling*

Month	1927	1928	1929
	in.	in.	in.
January	—	2.18	3.56
February	—	2.28	.53
March	—	1.45	2.92
April	—	3.16	6.40
May	—	2.48	7.80
June	—	4.65	—
July	—	3.69	—
August	—	2.77	—
September	—	3.65	—
October	—	2.34	—
November	6.77	1.88	—
December	3.55	2.53	—

SOIL

The soil on which the forest planting is located is classified by Hopkins *et al.* ('17) as upland prairie soil, varying from brown silt loam to black clay loam. An idea of the physical nature of the soil at different depths can be obtained from the wilting coefficients given in table II. From them it can be seen that the soil varies from clay loam at the surface levels to a fine sandy loam at the lower levels. The finer soil varies from two feet under ash to three feet under pine, larch, and maple and four feet under oak. This is followed in each case by a transition zone of loam, one foot in thickness beneath which fine sandy loam and sandy loam are encountered.

TABLE II. *The wilting coefficients of soils under different species of trees*

Depth	Green ash	White pine	Larch	Silver maple	White oak
ft.					
1	15.2	15.0	15.7	15.9	14.3
2	15.2	15.9	15.6	15.9	15.0
3	13.5	15.4	15.5	15.9	17.3
4	9.9	11.0	11.0	13.9	16.1
5	8.8	8.5	9.5	9.8	12.7
6	9.1	8.5	9.0	7.3	9.3
7	—	—	—	—	9.9
8	—	—	—	—	9.7

AVAILABILITY AND UTILIZATION OF WATER

The relative amount of available moisture which represents the amount of water in excess of the wilting coefficient for each foot at each sampling is shown in table III. Samples were taken in most cases down through the foot in which wet soil appeared. The gradation between the drier soil and the wet was very sharp, the capillary fringe ranging up to several inches. This zone of wet soil is correlated with the water table in the spring when the water table was rising and before the trees started using large amounts of

TABLE III. *Relative amounts of available moisture in soil under different species of forest trees at different times. Figures in parentheses indicate total percentage of water*

Kind of tree	Depth of soil sample	Relative amounts of soil moisture											
		1927	1928								1929		
		Nov.6	Mar. 5	Mar. 25	Apr. 10	May 1	May 26	June 11	June 24	Nov.12	Mar. 9	Apr. 6	May 14
	ft.												
Ash	1	20.5	22.2	20.5	21.4	—	14.2	19.3	20.04	21.8	31.5	21.3	—
	2	15.8	15.0	13.7	14.2	—	11.6	14.2	14.3	4.7	15.7	13.8	—
	3	10.5	11.7	11.8	11.8	10.7	12.7	14.2	13.6	4.0	10.4	15.3	—
	4	9.7	6.6	9.7	9.1	7.4	6.0	11.1	8.9	3.1	5.1	11.5	—
	5	11.9	7.4	9.7	*	1.7	4.1	4.9	3.3	-2.3	3.8	8.7	—
	6	7.3	6.9	11.7	*	7.8	6.0	4.2	3.3	5.3	5.3	*	—
	7	—	*	*	*	*	*	*	—	—	(11.5)	*	—
Pine	1	15.3	19.4	16.7	21.6	—	15.0	15.1	12.9	7.7	36.7	16.4	20.6
	2	6.5	14.3	13.8	15.2	12.9	10.6	9.5	9.4	3.7	13.8	13.5	15.9
	3	10.4	13.3	12.6	12.8	11.6	11.1	10.9	12.9	7.1	15.1	14.9	15.5
	4	13.1	12.0	11.8	15.1	12.1	10.5	13.6	14.6	7.6	18.3	16.2	17.5
	5	12.3	18.2	11.7	*	*	*	12.7	14.2	8.9	16.5	16.1	15.7
	6	11.5	*	*	*	*	*	*	*	8.9	12.7	*	*
	7	(19.3)	*	*	*	*	*	*	*	(19.9)	*	*	*
	8	(18.1)	*	*	*	*	*	*	*	*	*	*	*
Maple	1	15.8	19.9	17.5	20.5	—	14.6	17.0	16.4	20.6	21.6	19.9	18.7
	2	11.2	18.1	16.7	14.2	13.0	13.4	12.6	11.6	10.5	11.9	12.4	14.4
	3	11.8	10.8	14.0	14.2	15.0	13.1	11.4	13.1	9.6	12.6	15.4	13.9
	4	13.4	16.3	16.6	*	10.4	11.3	11.3	13.0	7.4	12.5	13.7	14.0
	5	13.0	20.2	16.5	*	*	9.7	8.2	12.1	3.1	13.1	21.0	*
	6	12.5	*	*	*	*	*	*	*	1.5	*	*	*
	7	—	*	*	*	*	*	*	*	(9.9)	*	*	*
	8	—	*	*	*	*	*	*	*	(11.0)	*	*	*

TABLE III (*continued*)

Larch	1	12.8	18.7	18.0	17.6	—	—	13.6	11.0	—	28.9	18.0	—
	2	8.8	16.3	14.7	15.8	—	11.0	9.3	8.5	—	15.3	14.0	—
	3	9.4	18.4	13.4	13.7	11.1	10.4	9.8	10.9	—	11.0	15.0	—
	4	5.9	22.2	18.6	15.8	10.6	6.7	5.2	10.7	—	3.5	14.8	—
	5	3.3	—	13.7	*	*	9.9	5.6	4.4	—	1.7	8.1	—
	6	4.2	—	*	*	*	*	5.9	—	—	3.7	6.7	—
	7	—	—	*	*	*	*	*	—	—	(12.9)	*	—
	8	—	—	*	*	*	*	*	—	—	(12.4)	*	—
	9	—	—	*	*	*	*	*	—	—	(11.2)	*	—
Oak	1	14.8	17.3	15.7	17.9	—	15.8	16.1	15.0	12.4	23.8	15.9	—
	2	12.9	14.3	13.2	17.2	—	13.1	14.5	10.6	1.5	13.2	15.9	—
	3	10.8	13.7	14.9	17.6	14.6	14.2	13.6	9.8	5.9	11.3	15.3	—
	4	9.9	17.9	16.1	*	15.9	14.3	12.8	12.5	6.0	9.7	8.3	—
	5	10.2	18.3	18.0	*	*	15.7	13.8	11.9	.8	2.5	7.7	—
	6	8.9	*	*	*	*	*	*	*	.6	2.8	*	—
	7	7.0	*	*	*	*	*	*	*	1.9	4.1	*	—
	8	5.0	*	*	*	*	*	*	*	3.4	2.7	*	—
	9	(14.3)	*	*	*	*	*	*	*	(17.0)	—	*	—
	10	(18.0)	*	*	*	*	*	*	*	(17.6)	—	*	—

* Wet soil, water table.

water, but when it was receding the removal of water below the water-holding capacity of the soil was dependent on the active roots in such layers. From the data in table III, it can be seen that as the water table receded the water content of the soil was reduced a great deal below the water-holding capacity of the soil. With available water in the upper layers of soil, root growth would not be stimulated to penetrate rapidly the lower layers as the water table receded. This would preclude the presence of roots living in saturated soil for several months, as the water table fluctuated from: 4 ft. down to 7 ft. under ash; 4 ft. down to 8 ft. under pine; 3 ft. down to 8 ft. under maple; 4 ft. down to 9 ft. under larch; and 3 ft. down to 10 ft. under oak.

From these results it can be seen that under ordinary conditions in the tall grass prairie region established trees have a constantly available supply of moisture.

In only one instance was the percentage of moisture found to be below the wilting coefficient. On November 12, 1928, for the fifth foot under ash a value of — 2.3 was obtained for the available moisture. It can be seen that there was very little available water at this time below the surface foot. At this depth under ash, gravel was encountered at times, and apparently this sample struck one of these patches, hence the low percentage of water and has no real significance.

No samples were taken under larch November 12, 1928, due to lack of time. At the time of the last sampling, May 14, 1929, the short soil tube broke while the second set of samples was being collected, thus limiting the samples to pine and maple.

In order to compare the relative amounts of water used by the different species of trees between the times of sampling, the available moisture in the first four feet of soil was used. The majority of the roots as was shown by ditches dug near the trees were in this region. To eliminate the unknown amounts of water in the wet soil at deeper levels it was necessary to limit this comparison to the first four feet. Where comparisons to deeper levels can be made the same tendencies toward water utilization are observed.

Whereas the rainfall from November to March in 1927–28 was nearly twice that for the same months the following winter, the accumulation of water in the first four feet was only about half as much. The water table rose more rapidly and reached a higher level during the spring of 1928 than it did the next spring. The presence of large amounts of duff under pine and larch did not seem to affect markedly the accumulation of water. Judging from these results the most important factors in water accumulation during the winter would seem to be the kind of precipitation, that is, rain or snow, the rate of precipitation, and the condition of the soil, whether frozen or not when precipitation occurs.

A comparison of the fluctuations of moisture content under the different species during the spring, summer and fall gives an index of the time when the most water is used and also the relative amounts used. Between March

5th and 25th little fluctuation was observed except under larch and here the moisture content was reduced over twice as much as under any other species. This species had evidently started using water although visible leaf growth did not occur until early in April. Leaves appeared on larch, maple and ash during April and their effect on the removal of water is very noticeable as may be seen from a comparison of the last readings in March and May. Larch used the most water, ash and maple a medium amount, and pine and oak the least. The oak leaves appeared during the latter part of May, and during June it was the only species to remove a noticeable amount of water. During this period in which the heaviest rainfall of the year occurred the moisture content under ash, pine and maple increased while it remained practically constant under larch. From June to November, ash, pine and oak removed about equal amounts of water, while maple removed much less.

For the entire season, March to November, the different species removed water from the soil in the following order: Oak most, pine, ash, and maple. Samples not being taken under larch in November prevents a direct comparison between it and the other trees for the season. However, with the exception of oak, larch removed more water during the period between March and June than the other species did during the entire season.

Soil Acidity

There was a wide range in the pH of the soil under different kinds of trees although the soil reached a fairly constant value at a depth of six feet as is shown in table IV. The soil under maple was least acid, whereas the surface foot was very acid under larch, pine, and oak. Acid soil extended to the greatest depth under oak.

Table IV. *The pH of soils under different species of trees*

Depth	Silver maple	Green ash	Larch	White pine	White oak
ft.					
1	5.40	4.95	4.30	4.20	4.45
2	6.40	5.10	4.90	4.80	4.55
3	6.70	6.10	5.40	5.90	4.80
4	7.20	7.10	7.20	6.70	5.35
5	7.80	7.80	7.75	7.20	6.70
6	7.75	7.70	7.80	7.60	7.90
7	—	—	—	—	7.90
8	—	—	—	—	7.80

Discussion

The ash, pine and larch considered in this paper were planted by Burrill in 1871. After the trees had become established they were thinned to rows eight feet apart with the trees four feet apart in the rows. The ash failed to develop uniformly and either died or were blown down by storms until

the stand at the time of this study was very irregular. In taking the soil samples it was impossible to find a satisfactory location where the trees were standing as thickly as they were in the original planting. There was also more ground cover of herbaceous plants and these facts may explain some of the irregular fluctuations in soil moisture under this species. In all other cases the trees were standing 4 by 8 feet apart which would assure a fairly uniform root distribution and utilization of water. With the exception of ash, there was very little ground cover due to the density of the stand. The original planting of larch extended into a poorly drained area. The larch in this portion of the plot died out according to Burrill because of the excessive moisture in the soil. Though larch used a large amount of water, it required a well-drained soil in which to grow.

The white oaks and silver maples under which samples were taken were between twenty-five and thirty years old. Their root systems were well developed as is shown by the amounts of water they removed from the soil.

It is impossible from the data collected to evaluate the effect of the different species on soil acidity; however, there are several important contributing factors that need further investigation. The decomposition of the needles under larch and pine would tend to make the upper layers of soil more acid. Schreiner and Skinner ('11) have shown that organic acids are washed from the leaves and trunks of some trees, and in the case of oak which is known to produce a large amount of organic acid the pH of the soil would probably be affected. Little is known about the calcium requirement of different trees. Differences in elevation and consequently in leaching are important factors.

The fluctuation of the water table is apparently not a factor, for regardless of its fluctuation the pH becomes quite uniform at six feet. It must also be remembered that the higher portion of the area was cropped for a number of years before the trees were planted.

Summary and Conclusions

Soil samples to a depth of as much as ten feet were taken at various times from November, 1927, to May, 1929, under five species of trees grown in pure stands on prairie soil. The moisture content, wilting coefficient, and pH of the soils were determined.

Water was found to be removed from the soil most rapidly by all species studied, except white pine, at about the time new foliage is produced.

Larch, white oak, and white pine removed more water from the first four feet of soil during the growing season than green ash and silver maple.

Soil samples to a depth of ten feet under white oak, nine feet under larch, eight feet under silver maple and white pine, and seven feet under green ash, show that the moisture content of the soil to these depths is affected by the trees. The water table fluctuated from three and four feet down to these depths, thus the trees had a constant source of water from the water table.

The soil was more acid to a greater depth under white oak, with decreasing

acidity under white pine, larch, green ash, and silver maple in the order named.

Regardless of differences in the fluctuation of the water table the soil reached a fairly constant pH at six feet under all species.

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PLANT DISTRIBUTION AS INFLUENCED BY SOIL HETEROGENEITY IN CRANBERRY LAKE REGION OF THE ADIRONDACK MOUNTAINS[1]

VERNON A. YOUNG

New York State College of Forestry, Syracuse, New York

Since the classical researches of Liebig, the father of agricultural chemistry, students have recognized that the chemical factors of the soil play a major rôle in crop production. As a result of this interest which was also correlated with an economic need, agricultural soil science has at the present time attained a high degree of development. Innumerable soil samples obtained from both large and small areas in North America which offered external evidences for crop production have been analyzed with the view of evaluating their analytical composition relative to plant growth. Little attention, however, has been paid to the analytical composition of areas and regions carrying natural vegetation unfit for agricultural purposes. Students of botany and forestry have not in the past kept pace with the development of agricultural soil science because they have been slow to recognize the importance of the soil as a major factor in the profound differences of growth and distribution of natural vegetation in regions of similar climatic conditions. Such a state of affairs has taken a decided change since the beginning of the 20th century with Warming and Ramann emphasizing the importance of the soil as an important factor in plant growth and distribution. Warming ('09), was the first to classify the plants in relation to the chemical factors of the soil in which they grow, while Ramann ('11), was the first to initiate the study of forest soil science in forestry.

In this country Hilgard ('06), pointed the way toward a scientific study of the chemical constituents of the soil in relation to the distribution of native vegetation. Hilgard's conclusions were soon confirmed by the data obtained by such investigators as Coville ('10), Fernald ('07, '19), Shantz ('11), and Wherry ('22), of America and Arrhenius ('20), Atkins ('22), Braun-Blanquet ('24) Christopherson ('25), and Olsen ('23), of Europe. Their findings clearly indicate that a definite relationship exists between the chemical and physical composition of the soil and the distribution of plants and plant communities.

The papers just cited as well as others had a far-reaching influence in calling the attention to students interested in various phases of plant growth. The

[1] The publication of the extra pages, tables and figures in this article has been made possible by funds other than those of the Ecological Society of America.

need of additional investigations relative to the physical and chemical factors of the soil that might influence plant growth and plant distribution became definitely evident. As a result, considerable investigation followed, but only those papers pertinent to the present investigation will be discussed.

Griffith, Hartwell and Shaw ('30), were among the first investigators in forestry in this country to follow the more modern procedure of determining the rôle of the soil in relation to forest growth and development. They concluded from their studies that successional development of certain forest species is definite areas were highly correlated with edaphic conditions of the habitat. Romell and Heiberg ('31), emphasized the importance of the physical composition of humus as a factor in the distribution of certain forest species. These data, in many respects, paralleled the data obtained by the writer [2] from a critical study of the chemical factors of the soil which influenced the distribution of desert vegetation in the old Bonneville Lake Basin of the western United States, which occupied areas of Nevada, Utah and Idaho. Here sub-irrigation, the lowering of the water table, erosion and deposition of soil brought about chemical changes in the substratum and a change in dominant species occurred. In addition, the data obtained in the Bonneville Lake Basin clearly showed that the physical and the chemical composition of the soil not only determine the species that the soil will carry in transitional zones but also separate pure communities by sharp boundaries. In many cases these differences were apparently of a permanent nature due to the original heterogeneity of the soil since unproductive spots are found in the agricultural fields of the supposedly uniform areas after many years of cultivation.

With the data of the above investigations in mind, the writer was inspired to make a quantitative study of the chemical and physical factors of the soil in relation to plant growth and distribution in limited areas of the Cranberry Lake region in the west central part of the Adirondack Mountains, where the virgin forest as well as other natural vegetational areas show a high degree of heterogeneity. It is, therefore, the primary purpose of the present investigation to determine if soil heterogeneity is correlated with this highly diversified vegetation, or if the pure and mixed communities are distributed over fairly large areas because of random distribution due principally to the activities of climatic and biotic agents. As stated above soil heterogeneity is the primary purpose of this investigation, nevertheless the effect of plant succession in small limited areas in relation to soil change and plant development became a part of the general study.

Cranberry Lake Quadrangle; the Region Investigated

The region investigated comprises the immediate areas surrounding Cranberry Lake in the west central part of the Adirondack Mountains. Cranberry Lake is a partially artificial body of fresh water occupying an area of

[2] Data to be published in Harris Memorial Papers by University of Minnesota.

about 11 square miles. Approximately one-fourth of this area was added after a dam 14 feet high was built across the discharge channel of the lake. A brief description of the topographic, climatic and vegetational features of the region is, therefore, pertinent to the discussion.

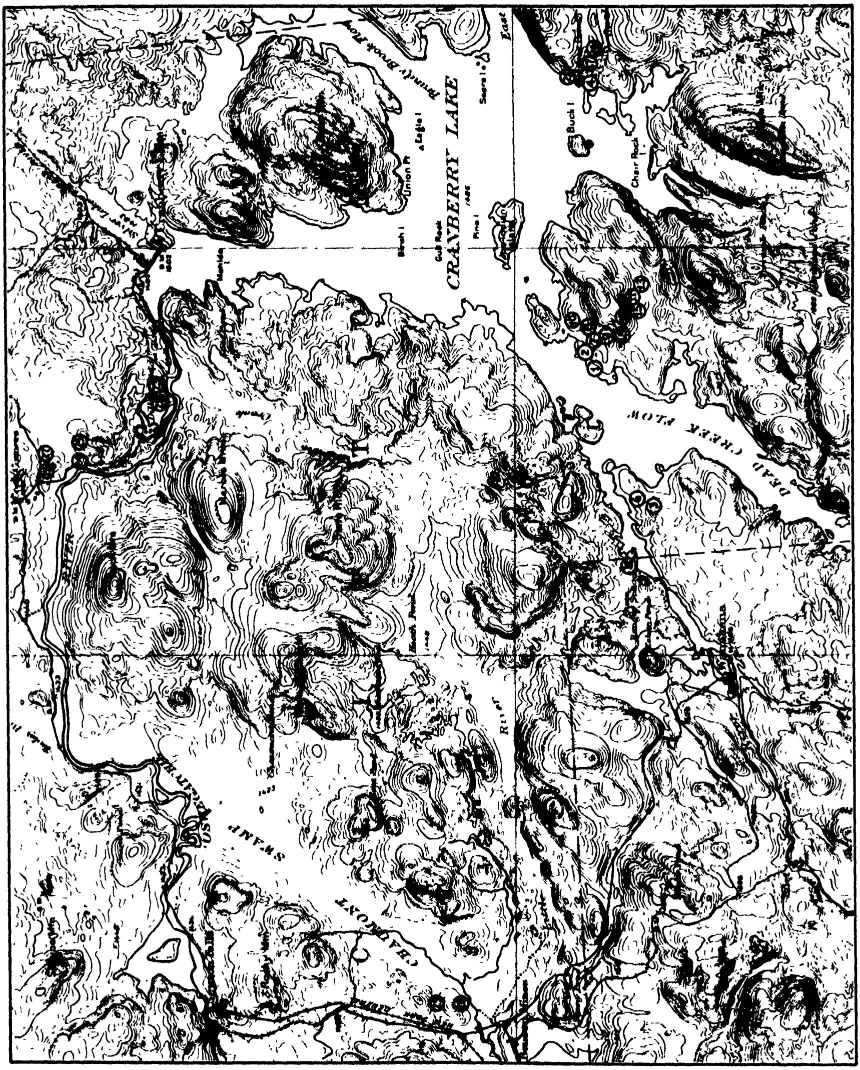

Fig. 1. Map of Cranberry Lake region showing the location of the stations.

Topographic Features

Cranberry Lake is approximately 1500 feet above sea level, in a region, which like most of the Adirondacks, was severely glaciated. The surface features, as a whole, are highly variable, being similar to most glaciated areas of the northeastern United States. It is occupied by several large hills with

abrupt to long descending footslopes which drain either into depressions or streams flowing into Cranberry Lake. In several localities prominent eskers have profoundly influenced the topography of the region. Numerous large and small depressions are widely distributed and carry either swamp or bog vegetation depending upon the degree of free drainage. Among the many streams which empty into Cranberry Lake, the Oswegatchie River is the most important in size and area drained. Innumerable large and small granite boulders cover the surface of the region.

Climate

The climate is decidedly cool according to Stickel ('31), who made a comprehensive study of the meteorological conditions. He reports —30°F. as the lowest and 85°F. as the highest air temperature with extreme daily variations in both temperature and relative humidity. The wind movements are quite similar to those of other mountainous areas of New York and no unusual velocities have been reported. The amount of precipitation which averages from 45 to 50 inches annually is similar to that of the Great Lakes region. Such abundant precipitation, which is quite uniformly distributed throughout the year, would definitely indicate that moisture should not be a limiting factor in plant growth and distribution except in extremely small areas where edaphic conditions are extreme.

Soil and Vegetation

The soils are of a podolized nature and heterogeneous in the sense that they show differences from locality to locality, as well as within each habitat throughout the entire region studied. The original soil material deposited by the retreat of the glaciers was principally sand and up to the present time no clay deposits (as based upon the standard clays) have been found. The soils as a whole are raw and cold as compared to the non-glaciated soils of the United States. They are also quite acid; in fact, none seems to show a basic reaction. In certain localities where washouts have occurred, several feet of the exposed substratum reveal glacial deposits of soil varying in size of particles from silt to very coarse sand.

In many areas the sand substratum lies near the surface while in others peat or muck forms deep layers. The most notable example of a deep peat deposit is found in Esker Pond (fig. 2), a small glacial lake lying at the base of an esker, where peat has accumulated to a depth of 27 feet. Below this a fine, glacial sand is present. Soil erosion caused by the destruction of the ground cover by fires and severe logging operations has been quite general in certain areas, and changes in the physical and chemical composition of the soil would be expected. The humus layer varies widely as to depth from less than one inch in the burned areas to 26 inches in the stands of old white pine.

The forest as a whole is typical of the vegetation found in the lower edge

of the upper altitudinal zone of the western half of the Adirondacks. This vegetation is diverse, its composition depending upon the physiographic features [3] of the region as well as upon the physical and chemical constituents of the soil. Often small areas carrying either shrubs or herbs, or both, occur

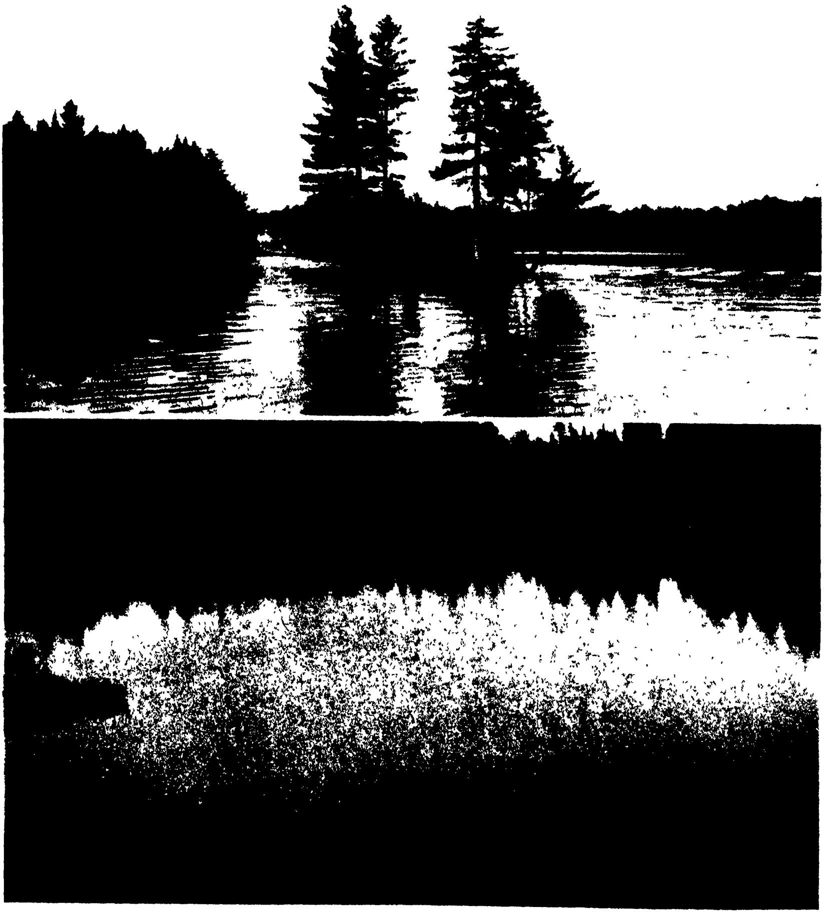

FIG. 2. Cranberry Lake with forests. Trees to the water's edge (above). Esker Pond (below) with black spruce showing height gradient.

in an otherwise uniform type of forest. Again, a single hardwood or softwood species may form a comparatively pure stand of limited extent within a larger one supporting a mixed forest, while in a few cases the vegetation can be segregated into zones.

In certain localities units of the virgin forest have escaped the destructive

[3] Frost pockets have been reported in certain areas.

effect of forest fires and logging operations. A few of these small areas are still supporting huge white pines, *Pinus strobus* L., which may be remnants of an earlier forest which carried a higher percentage of this species. Many white pine saplings are widely distributed over the region, while in two very small areas stands approximately 50 years old are making fair growth. The distribution of these white pines will later be discussed in more detail.

Forest fires during the last 50 years have destroyed certain portions of the natural vegetation affecting modification in soil and vegetational composition. As a result of these conditions, successional stages varying from the herb-shrub to sub-climax stages are evident. In localities where lumbering operation have been severe, a highly diversified vegetation is developing due in part to the opening up of the forest canopy and to changes in soil cover and in drainage.

In the areas where the virgin forest still remains and appears to be a climax,[4] the vegetation is a mixed hardwood-softwood stand composed of the following dominant species; red spruce, *Picea rubra* Link., eastern hemlock, *Tsuga canadensis* (L.) Carr., white pine, *Pinus strobus* L., of the softwoods, and beech, *Fagus grandifolia* Ehrhart, yellow birch, *Betula lutea* Michx. and sugar and red maples, *Acer saccharum* Marsh., and *A. rubrum* L., of the hardwoods. White pines are quite limited in distribution and number, but in certain localities they grow unusually large; therefore it would seem wise to include them among the dominant species. Other tree species associated with these dominants are, pin cherry, *Prunus pennsylvanica* L., striped maple, *A. pennsylvanicum* L., and balsam fir, *Abies balsamica* (L.) Mill. The size of the balsam fir is apparently correlated with certain physiographic features since it is a small tree in the swamp and bog areas but quite large in a few local upland areas where it suggests dominance. Besides the reproduction of the tree species, hobble bush, *Viburnum alnifolium* Marsh., is the principal shrub except in the more open areas where Rosaceous, Caprifoliaceous and Ericaceous shrubs occur. Ferns are abundant in the Cranberry Lake region, 11 genera and 17 species have been collected. The wood fern, *Aspidium spinulosum* (O. F. Miller) Sw., polypody, *Polypodium vulgare* L., brake, *Pteris aquilina* L., and sensitive fern, *Onoclea sensibilis* L., are the most common in the virgin forest. The hay-scented *Dicksonia punctilobula* (Michx.), Gray, maidenhair, *Adiantum pedatum* L., cinnamon, *Osmunda cinnamomea* L., and oak, *Phegopteris dryopteris* (L.) Fée., ferns are quite abundant in wet areas where the shade is not too dense. One of the relatively rare ferns of the region is the royal, *Osmunda regalis* L., which grows in a few localities along the lakes and stream banks. *Equisetum sylvaticum* L. was the only species of the Equisetaceae observed but it is quite common in wet areas. Among the club-mosses, *Lycopodium lucidulum* Michx., and ground pine,

[4] The climax forest of the Cranberry Lake region has not as yet been definitely established; therefore the terms virgin and climax forest will be used synonymously for the most highly developed mesophytic type of vegetation.

L. complanatum L. var. *flabelliforme* Fernald, are the more common, while *L. clavatum* L., *L. annotinum* L., and *L. obscurum* L. var. *dendroideum* Michx., occur sparingly throughout the region. The herbaceous vegetation is made up of several species which are seasonal and often sparsely scattered. Among the more important are bunchberry, *Cornus canadensis* L., Canadian mayflower, *Maianthemum canadense* Desf., and common wood sorrel, *Oxalis acetosella* L., which are the dominant species of the forest floor, while wild sarsaparilla, *Aralia nudicaulis* L., shin leaf, *Pyrola elliptica* Nutt., Indian cucumber root, *Medeola virginiana* L., *Clintonia borealis* (Ait) Raf., starflower, *Trientalis americana* (Pers.) Pursh, variegated trillium, *Trillium undulatum* Willd., and erect trillium, *Trillium erectum* L., are the subdominant species.[5] Several species of sedge, moss, liverworts and algae common to the Adirondack Mountains grow in certain areas, but are not especially important in the present paper.

The above description of the topographic and vegetational features of the Cranberry Lake region have been emphasized with the view of presenting the need of habitat studies in order to determine if soil heterogeneity is associated with differences in vegetation. The present paper is based on the data of soil samples obtained during the summers of 1931, 1932, and 1933, among the roots of plants growing in comparatively pure stands as well as in mixed communities. Only a brief description of the topographic, soil and vegetational features of each habitat will be given. The approximate location of each station (for convenience the term station will be used synonymously with habitat) can easily be determined by noting the figures on the map of the Cranberry Lake region.

Stations Located in the Hardwood-Softwood Virgin Forest

Station 1. Hardwood-Softwood Forest. (Most typical)

The community supported by this habitat is the most representative hardwood-softwood forest in respect to site, size, species and reproduction in the Cranberry Lake quadrangle. As a whole it closely approximates in composition the virgin forest previously described. Both the herbaceous and woody species have well developed root systems, those of the former in most cases penetrating the enriched layer of the soil, while those of the latter often occur 18 inches below the surface. In all habitats soil collections were made from profiles distributed in four different places in the habitat in order to obtain representative samples. The profile in the podolized soil as stated on page 171 includes a humus layer,[6] leached layer, enriched layer and the substratum. The humus varies from 2–5 inches in depth. The surface inch is quite

[5] Henceforth the common name of each species will be used after the scientific name has been introduced.

[6] The term humus as used in the present paper includes that part of the surface above the leached layer.

coarse; the degree of decomposition varies, however, with depth. The leached layer is approximately 2 inches thick, while the enriched layer may vary from 1–3 inches in thickness. Below the enriched layer a sand of medium texture (the first 3 or 4 inches usually including considerable organic matter) forms the substratum to a depth of 18 inches, where it becomes coarse and open.

Station 2. Hardwood-Softwood Community on Cranberry Lake Shore

The most highly developed virgin forest community observed during the investigation is supported by this habitat. Many unusually large hemlock and red spruce tower above the hardwoods. Practically no tree reproduction occurs. The roots of the herbaceous vegetation lie near the surface, seldom extending into the enriched layer, while those of the woody species penetrate a few inches deeper. The soil profile is composed of the following portions: humus 14 inches deep, the degree of decomposition varying with depth; leached layer from 1–2 inches thick; enriched layer varies from 1–3 inches in thickness. The substratum below the enriched layer gradually changes from a fine brownish yellow to a light grayish coarse sand at approximately the second foot level.

Station 3. Hardwood-Softwood Community

This community is in a locality where few softwoods grow and the hardwoods are very large. Reproduction of all tree species is very limited because of the intense shade. The herbaceous cover is composed principally of wood sorrel and wood fern. The layers of the soil profile are humus 2–3 inches deep, dark in color, and well decomposed; leached layer is 1–2 inches in thickness; enriched layer approximately .5 inch in thickness. Below the soil contains considerable organic material to a depth of approximately 16 inches where the substratum becomes coarse and open.

Station 4. A Hardwood-Softwood Island Habitat

A small island in Cranberry Lake comprises this habitat with the water lashing its shores within a few feet of the surface soil. Both the hardwood and softwood trees are quite small compared with those in the other virgin forest areas, but the herbaceous vegetation is typical. The soil varies considerably in color and structure as compared with the other habitats. The soil profile shows a well decomposed humus layer 6 inches thick, a leached layer varying from 1–4 inches in thickness, and an enriched layer approximately 2 inches thick, very dark and extremely hard. A thin hardpan as well as the existence of dark yellow horizontal strata in the first 18 inches of sand below the enriched layer is outstanding.

Station 5. Pure Softwood Community

This very small community (30 ft. square) of pure red spruce growing on a ledge rock habitat is rooted in soil less than 3 inches deep and no definite

enriched layer could be determined, although a very thin leached layer was apparent in a few places. The trees are medium sized and their roots spread widely over the rock floor, taking advantage of cracks and breaks in the ledge to obtain anchorage. Practically no herbaceous plants grow in this shallow soil and dense shade.

Station 6. Beech-Yellow Birch Community

A small area supports this comparatively pure stand of beech and yellow birch. The beech trees are the largest individuals observed in the region. Hemlock, red spruce and hard maple are abundant in areas surrounding the habitat. Club mosses are practically absent, but the herbaceous flora as a whole is similar to that of the virgin forest. The soil is well drained. The soil profile shows the following aspects: well decomposed humus less than 2.5 inches thick; a leached layer less than 2 inches thick; and an enriched layer of 1 or 2 inches very dark in color. Considerable organic matter is present in the first 3 or 4 inches of sand below the enriched layer, but disappears as the substratum becomes coarse open sand 15 inches below the surface. Leaf litter in this habitat is apparently converted very quickly into a decomposed form of humus.

Station 7. Hardwood-Softwood Community Bordering Large Swamp

This community is supported by a habitat which is bordered on three sides by a swamp forest, an upland forest forming the other boundary. The habitat is well drained and covered with large granite boulders. It was selected in the hope that the soil characteristics might reveal a chemical composition transitional between the swamp and upland vegetation. The vegetation as well as the soil profile is roughly similar to those of the virgin forest.

Station 8. Hardwood-Softwood Swamp Community

This community occupies the highest elevation in a large swamp approximately one-quarter mile southwest of station 9, a black ash community. With the exception of beech, all the trees common to the climax forest are present, including the arbor vitae, *Thuja occidentalis* L. Considerable reproduction is evident for all species. A dense mat of sphagnum moss, approximately 3 inches deep, covers the site. Several sturdy bushes of swamp honeysuckle, *Lonicera oblongifolia* (Goldie) Hook., grow on slightly elevated spots. A few dwarf raspberries, *Rubus triflorus* Richards, grow on partly decayed fallen trees or in the crotches of living tree trunks. Hobble bush is absent, but cinnamon fern is abundant. Only a few herbaceous species common to the virgin forest are present, but several species of sedge grow luxuriantly. The first two feet of the soil profile consists principally of organic matter and a fine sand layer; the former consisting of 4–6 inches of raw to partially decomposed organic matter and the latter extending 25 inches below the surface where coarse sand occurs. Soil samples taken 4 feet below the surface showed no signs of a hardpan layer.

Station 9. Black Ash Community

The site which supports the black ash community is located near the origin of the swamp just described. It is confined to a long narrow strip of ground approximately 60 yards wide and 300 yards long, which is slightly lower in elevation than the surrounding area. Water drains quite freely through the habitat during practically the entire growing season. Black ash, *Fraxinus nigra* Marsh., is the dominant species, but red spruce, balsam fir, hemlock and yellow birch occur sparingly, while arbor vitae is quite abundant. The entire community has suffered a high mortality in the past; nevertheless, reproduction has been normal except in the case of ash. There are practically no middle size black ash, but a heavy reproduction of young saplings. Ring counts of several saplings indicate very slow growth, since they were 14 and 15 years old with diameters less than one-fourth inch. Only two shrubs, wild raisin, *Viburnum cassinoides* L., and dwarf raspberry, are able to maintain normal growth. Sensitive fern is abundant, while the oak fern grows in limited numbers at the base of tree trunks. The cinnamon fern is absent but forms dense stands near the margins of the habitat. Among the herbaceous forms, marsh blue violet, *Viola cucullata* Aiton, and deerhair sedge, *Carex virescens* L., are abundant, but species common to the surrounding areas are absent or very rare. The soil profile showed humus 12 inches deep, the upper 4 inches coarse but the lower 8 inches containing a high percentage of organic matter associated with considerable fine sand. At a depth of 12 to 18 inches a semi-hardpan layer occurs, while below this depth, as far as examined (30 inches), a stone-like hardpan impervious to water is present. The hardpan is light gray in color, with reddish tinges distributed through it. The sand layers of the profile appear to be of water deposited, accumulated by erosion over a long period of time. Because of the unusual nature of the soil profile, drainage and diversified vegetation, this habitat is one of the most interesting of the region.

Station 10. Old White Pine Community

This old dominant white pine stand occupies a very small habitat of less than 400 square feet and is quite characteristic of an island, since its surface is approximately 5 feet higher than the surrounding swamp forest rich in hardwood-softwood species. These white pines are very large (approximately 4 ft. in diameter) and between 300–400 years old. Because of their unusually dense foliage, very little light filters through to the forest floor, which is practically free of herbaceous plants and woody reproduction. Only a few red spruce and hemlock have been able to partially mature. The soil profile is one of the most highly diversified observed. The humus is 26 inches deep, the first 4 inches being coarse needle duff. Below this level the degree of decomposition is correlated with the depth gradient. The leached layer is 2 inches thick and almost white in color. The enriched layer varies from 2–4 inches in thickness and is almost black as well as very hard. Below this is a coarse sand.

Station 11. A Bog Community

This partially matured bog community is supported by a habitat located at the base of a large hill, on which the virgin forest was completely destroyed by fire in 1882. It occupies an area approximately 300 yards wide and 1200 yards long. The vegetation is definitely separated into zones due to successional developments. In the lowest part of the bog a dense growth of Ericaceous species forms the dense inner zone. Labrador tea, *Ledum groenlandicum* L., and *Chamaedaphne calyculata* L., indicators of a firm bog substratum, are the principal species. The water level, which varies with the season, is approximately 2.5 feet below the surface in this zone. Sphagnum moss still forms a mat among the shrubs, but the sedges are fast giving way to the woody species. Conifer invasion is very evident in the zone, with many small seedlings of black spruce, *Picea mariana* (Mill) BSP, and tamarack, *Larix laricina* K. Koch, obtaining a foothold, while here and there a white pine or red spruce seedling can be seen. Extending outward a few yards through a transitional area, black spruce becomes dominant and forms a definite zone. Toward the outer margin of the swamp, the black spruce zone gradually becomes dominated by tamarack which forms a zone over the larger part of the habitat. In the southeastern portion of the tamarack zone, the trees are extremely large and form a pure community (selected as stations 12 and 13) while to the southwest a young white pine stand (50 years old) sets up a sharp boundary (selected as stations 14 and 15) between the young tamarack and black spruce as indicated in figure 3. The white pine occupies slightly higher ground than the other zones. The leatherleaf and Labrador tea form a heavy undergrowth throughout the habitat, except in the white pine zone where they are completely absent. The herbaceous cover of the habitat is similar to that of other bogs in the region. The abundant white pine reproduction, varying in ages from 20 years old to small seedlings, is significant and would indicate that either a high mortality must occur or ultimately this species will become dominant. A study of the soil profile gave definite evidence that the bog had been filled in gradually, but that erosion material brought down from the surrounding hills since the forest fire of 1882 had played a more important rôle during the last 40 years than during any other period. Soil samples were taken at 2, 8, 14, 26 and 28 inches in each profile. The degree of decomposition was correlated with the depth gradient, the 14 inch layer being more decomposed than would have been expected in a bog where deposition was very limited. A thoroughly disintegrated peat was found 6 feet below the surface.

Stations 12 and 13. Pure Tamarack Communities

There are two distinct zones of tamarack in this habitat based upon size. Station 12 is located in the zone of smaller trees (fig. 3), while station 13 supports a stand of large mature tamarack. Practically no tamarack reproduction is evident, but red spruce reproduction is abundant, which definitely indi-

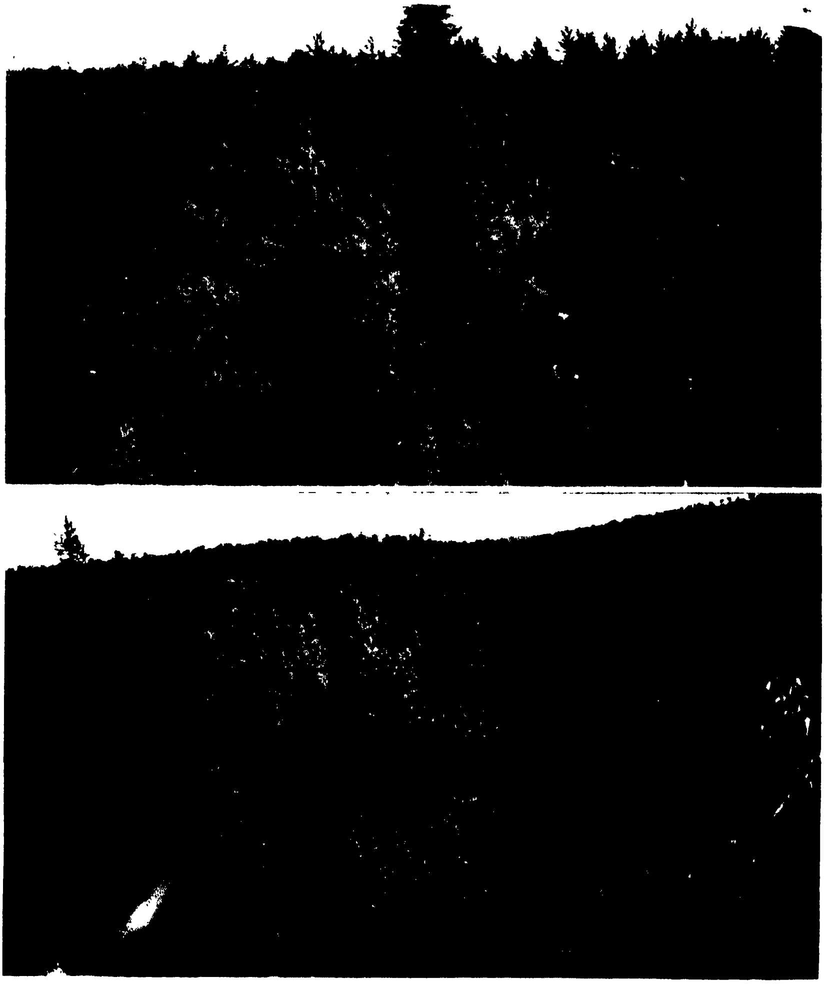

FIG. 3. Pine and spruce forests. White pine in the background (above) showing a sharp boundary from the young tamarack and black spruce. Red spruce and white pine approaching a dominant stage in a tamarack and black spruce bog (below), near station 12.

cates a severe invasion. The water level in station 13 is 6 inches lower than in station 12, otherwise their soil profiles are quite similar.

Stations 14 and 15. Young White Pine Communities

In station 14 the white pine forms a pure stand, while in station 15 red spruce and balsam fir are quite common. Reproduction of the white pine is prolific in both stations. It is quite apparent that the white pine saplings in station 11 grew from seed distributed from the pines of these stations. These white pine stands are important, because it is the only habitat of any size ob-

served in the Cranberry Lake region where young white pine is the dominant species.

The soil profiles are unusually interesting because the enriched layers are extremely thin (less than 1 inch) while the leached layers are 2 to 3 inches thick and very fine in texture. The humus layers are principally needle duff 4 inches deep. The substratum below the enriched layers is coarse sand.

Stations in Hardwood Forest Where Fires and Lumbering Operations Have Occurred in the Past

Station 16. Hardwood Climax Forest

A small dense community of beech and hard maple with practically no yellow birch has developed in this locality, the softwoods, if they were ever present, having been removed by lumbermen. Here a most prolific reproduction of beech and hard maple is making excellent growth. No softwood reproduction is evident and the herbaceous vegetation is limited in both species and number of individuals. The soil profile consists of a thin, well decomposed humus layer less than one inch thick; a leached layer less than 2 inches thick; and an enriched layer extremely dark in color and 2 inches in thickness. Below the first foot the soil is coarse sand.

Station 17. A Pure Bunchberry Community

This dense community of bunchberry showing vigorous growth and prolific reproduction is developed in an open area (25 square feet) in the hardwood forest. The soil profile consists of well decomposed humus 3 inches thick; a leached layer 1–2 inches in thickness and rather dark in color as compared with the leached layers observed in other habitats. The enriched layer, approximately 1.5 inches in thickness, is extremely dark and of fine texture. Roots of the bunchberries are primarily confined to the humus layer and only occasionally do they penetrate the enriched substratum.

Stations Distributed Over the General Region Where Fires Have Destroyed the Forest and Second-Growth Stands Have Developed

Station 18. Young Yellow Birch Community

The yellow birch community occupies a small area which carried a virgin forest prior to 1916, when it was severely burned. Numerous yellow birch, many fire cherry, a few red maple and aspens, both *Populus tremuloides* Michx. and *P. grandidentata* Michx., have secured a foothold in the area. As a result of the invasion the most severe competition is going on, which is in part indicated by the dense growth shown in figure 4. The floor of this area is practically free from shrubs and herbs because of the dense shade. However, Indian pipe, *Monotropa uniflora* L., finds the environment suitable to its requirements and two or three plants may be observed in a 5-meter quadrat.

The soil profile in many places is not definitely divided into the distinct humus, leached and enriched layers as observed in the virgin forest. A very thin but well decomposed humus layer is evident; the leaves apparently decompose very rapidly after coming in contact with the soil.

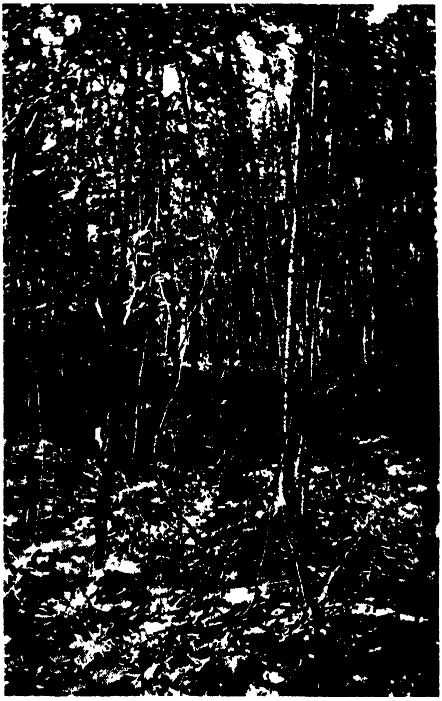

FIG. 4. Yellow birch forming a dominant stand in a habitat burned in 1916.

Station 19. A Mixed Hardwood Community

This community is supported in a well drained area, on which the virgin forest was burned in 1882. The dominant species are yellow birch, big-tooth aspen, hard maple and a few beech. A high mortality among these hardwoods is quite evident with some red spruce and balsam fir saplings surviving the competition. Many of the herbaceous species common to the virgin forests are invading the habitat. This community now represents the type of forest that station 18 will later support since the communities often slightly overlap each other. The soil profile is more definite than in station 18, as all the layers can be clearly differentiated. The humus layer in most places shows distinct variation as to raw and decomposed portions.

Station 20. Young Aspen Community

Big-tooth and trembling aspen are the dominant species of this 22 year old community, although yellow birch and hard maple are quite abundant in

certain small areas. The habitat was swept by a severe fire in 1908 and the forest was completely destroyed. The area is well drained and covered with numerous rocks varying from cobblestones to boulders. Competition among the species is severe and only a limited number of herbaceous or shrubby plants have been able successfully to endure the habitat.

The soil profile is quite similar to the one of station 19, except that the humus layer is very thin, often less than half an inch, and composed of rapidly decomposing leaf litter.

Partially Cultivated Community

Station 21. White Clover Community

White clover forms the dominant herbaceous species in a small habitat where the New York State College of Forestry Sophomore Summer Camp is located. The area supported in the past a forest typical of the region, but several trees were removed to provide ample space for the camp. Soil samples were taken in order to determine if the clover cultivation had influenced in any manner the composition of the soil as compared with the soil supporting natural vegetation.

Habitats Located West of Cranberry Lake Village in a Locality of Highly Diversified Topographic and Vegetational Features

Glacial deposits as well as stream cutting have affected a highly diversified topographic region in the neighborhood of Cranberry Lake. Several small lakes and low dry depressions occur between sandy ridges. The original forest in several areas has been destroyed either by lumbermen's operations or by fires, while in other areas the initial vegetation of unusual composition remains. The following stations are located in the latter areas:

Stations 22 and 23. Scrubby Softwood-Hardwood Community

These stations are situated on a long ridge where excavations exposed the soil profiles. Figure 5, a profile of station 23, shows the soil layers. The profile shows that the dark humus layer is approximately one inch thick; the leached layer 4 inches thick and the enriched layer 16 inches in thickness. The upper 3 inches of the enriched layer are almost black, while the lower 13 inches blend from a brownish yellow to a grayish yellow color with the depth gradient. This latter portion is a hardpan and when exposed to the air can be removed in small blocks. Below the enriched layer the sand is stratified with fine and medium textured grains indicating water deposits.

The vegetation in both habitats is highly diversified with a thin stand of dwarfed hardwood-softwood species, such as trembling aspen, black spruce and tamarack, competing for dominance, with balsam fir limited to a few individuals. Pussy willow, *Salix discolor* L., and pin cherry are sparingly distributed in the habitat. Such shrubs as shadbush, *Amelanchier canadensis*

(L.) Medic., and red raspberry, *Rubus idaeus* L., are common. Black huckleberry, *Gaylussacia baccata* (Wang) C. Koch, low sweet and sour top blueberries, *Vaccinium pennsylvanicum* var. *augustifolium* (Ait.) Gray, *V. canadense* Kalm, ground pine and brake fern, also are quite abundant. The herbaceous plants form a fairly dense growth. However, only those plants not common in the virgin forest will be mentioned, which are as follows: goldenrod, *Solidago rugosa* Mill., two species of hawkweed, *Hieracium aurantiacum* L., and *H. florentinum* All., fireweed, *Epilobium augustifolium* L., wild strawberry, *Fragaria virginiana* Duchesne, and a few sedges and grasses.

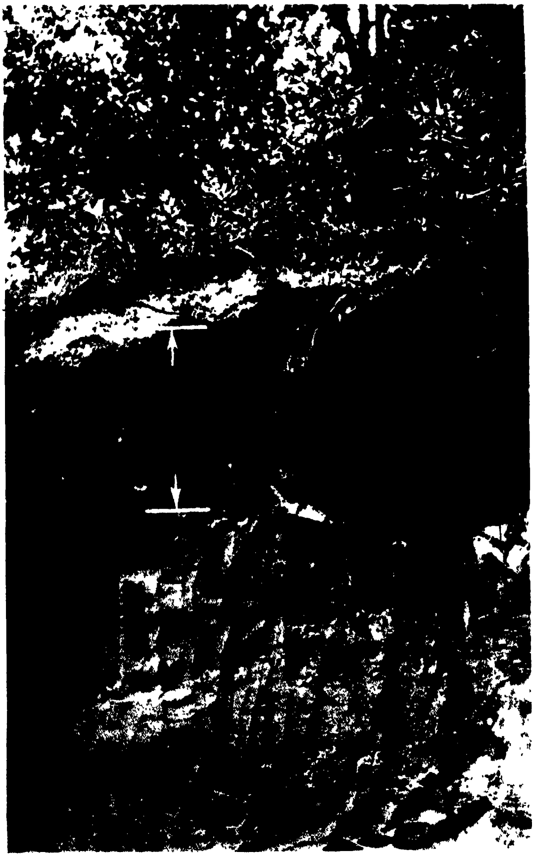

FIG. 5. A soil profile at station 23 showing the thickness of the enriched layer between the arrows. The layer is a hardpan.

Stations 24 and 25. Shrub and Herb Community

This community is located one mile west of station 23 on the same general elevation. The vegetation is characteristic of the sand plains of certain areas in the Adirondacks where scrubby aspen and dwarfy willows form the domi-

nant species, while a highly diversified herbaceous flora covers the ground. Among the important and abundant species not listed in stations 22 and 23 are: pearly everlasting, *Anaphalis margaritacea* (L.) B. & H., lousewort, *Pedicularis canadensis* L., and numerous small patches of mosses.

The soil profile is quite similar with those of stations 22 and 23 except the yellow portion of the enriched layer, which lies within eight inches of the surface and is a distinct hardpan.

Stations 26 and 27. White Pine-Shrub Community

The habitat includes an area of the large ridge one-half mile west of station 25 where a junction is formed between a large swamp and an open plain, the latter sufficiently fertile to grow pasture crops. The habitat is a typical open brush region supporting three vigorous white pines approximately 60 years old. A heavy reproduction of white pine and balsam fir seedlings in the habitat is of unusual interest. These seedlings are well protected by a heavy growth of shrubs common in sections 22–25. The herbaceous flora is not as rich in individuals as the stations located elsewhere on the ridge, but grasses form a sod while sedges are quite rare. The soil profile differs widely with those of stations 22–25, since the humus is principally sod and the leached as well as the enriched layers are very thin, approximately half an inch in thickness in each case. The first foot of soil contains considerable organic matter and no hardpan layer was observed in the profile. Station 25 is situated near the three white pines and 26 is located a half mile to the east in an area a few feet lower in elevation.

Stations 28 and 29. In a Region of Retrogression

The habitat located in this region is approximately one mile north of Benson Mines Village. In 1910, a heavy stand of dominant red spruce was carried by the land. During the following three years it was intensively logged and severely burned. Where the charred stumps fell and decomposed in the soil, dense mats of mosses are now growing. The first tree species successfully to invade the region was trembling aspen, in small patches where it grows very slowly. Between the aspen groves dense growths of hawkweed often cover the ground, while low shrubs typical of station 23 are found among them.

Station 28 is in a dense growth of hawkweed, and station 29 in an area spotted with dense mats of moss. In general the two soil profiles are quite similar, the humus varies from 1–2 inches in thickness; leached layers are approximately 1 inch thick, and the enriched layers vary from 1–2 inches in thickness. It is very evident that the region has undergone some drastic edaphic change, which may be correlated with the absence of certain microorganisms since the humus is very raw.

Methods

Soil Sampling

In order to obtain representative data of the soil properties under which the plants are growing, soil samples were taken from among the roots of the plants. It was impossible to take the soil with a soil tube or soil auger because of the rocky substratum. Instead large holes were dug with a spade to a depth of two or more feet, exposing a soil frontage where all of the layers of the profile could be studied and samples removed with a spatula without contamination. This method was laborious but very accurate, therefore it was used throughout the investigation.

As stated elsewhere, the soil samples taken in the profiles included the following divisions: humus layer, leached layer, enriched layer; the first foot layer which also includes the three layers just mentioned and the second foot layer. The name "leached layer" was applied by early soil investigators because of its supposedly low chemical composition and light grayish color. The enriched layer received its name because of its apparently high chemical composition and rich dark color. Four or more soil profiles were sampled at each station and all samples thoroughly mixed in order to obtain a representative composite of the area for the analytical data. This was necessary since the analytical data showed as the investigation progressed that the physical and chemical properties of the soil within a habitat varied somewhat in each area analyzed.

Soil Analysis

Methods used in the soil analysis are a modification of those introduced by Schreiner and Failyer ('06) in which water extracts were used. The soil samples were permitted to remain for six months in a drying room where they reached constant air dryness before the determinations were made. Therefore, all of the analytical data presented in the present paper are based upon air dry samples. This procedure was followed because of the uncertain effect of oven heat on soil. Furthermore, Bailey ('31) has established the fact that pH determinations are more reliable from air dried than from wet soil. Besides the mechanical analyses, the analytical and electrometric determinations made on the water extracts include calcium, manganese, aluminum, iron, hydrogen ion concentration and specific electrical conductivity.

Mechanical Analysis of Soils

The mechanical analyses of the soil were made according to methods outlined by Bouyoucos ('30).

Preparation of the Aqueous Extract

The analyses were carried out in the following manner: 40 grams of soil were weighed out to which 200 cc. of distilled water was added. Therefore 5 cc. of the filtrate represent approximately 1 gram of soil.

As the preliminary analytical determinations of the soil progressed, it became apparent that such elements as calcium, magnesium, manganese, potassium, phosphorus, aluminum, iron, sulfate and chloride were low and irregular in water soluble forms available for plant use. It was also evident from these analyses that aluminum was associated with certain elements in the hardpan layers of the soil. Nitrogen was comparatively high in the organic cover but low and irregular in the inorganic substratum. From these data it became evident, because of the low and irregular values among the elements, that several of these would be of little importance as criteria for the differences in the distribution of natural vegetation but a difference between the sum total of these ionic constituents would be significant. Therefore, in order to obtain this result the specific electrical conductivity measurement seemed to be the most logical method to employ to obtain a reliable measure of the total ionic constituents of the soil that would give total differences large enough to be trustworthy. Furthermore, the laborious method of separate analyses could be eliminated. On the other hand, a certain amount of quantitative analysis was necessary in order to determine the presence of aluminum and other associated elements which appeared to be correlated with hardpan formation, an important factor in the distribution of the vegetation of the region. It was possible to attain this end by making a quantitative determination for calcium in which the presence of aluminum as well as of other elements could be detected. In addition, the determination of the calcium content of the soil seemed pertinent, not only for the presence of aluminum but also to note its general distribution as well as its effect in relation to the degree of acidity in each layer of the soil.

Because of the unusual distribution of nitrogen in the soil and due to the fact that practically all of the woody plants extend their feeding root systems for some distance into the inorganic substratum (except in bogs and swamps), it would seem logical to conclude that this element alone could not account for the major differences in plant distribution observed in the Cranberry Lake region. However, the writer has not lost sight of the theory that the nitrogen content of the forest soils is generally recognized to be one of the factors which most strongly influences the growth of forests, especially where bogs and swamps are involved. Nevertheless, the availability of this element in desirable forms for plant use is highly dependent upon the environment in which it occurs and its potential value may be very limited. Certain of these limiting factors seem to be associated with the nitrogen content of the soils in the Cranberry Lake region, the data of which will be treated in a later paper. Therefore, no further determinations were made for nitrogen in the present investigation beyond the preliminary stages other than the specific electrical conductivity measurements which seemed sufficient for the problem involved.

Determination of the Water Soluble Calcium, Iron, Managanese and Aluminum

Quantitative determinations were made of the water soluble calcium which is available for plant use. The method used is the one described by the Association of Official Agricultural Chemists ('25) with the following departures: (1) In the absence of either iron or aluminum the PO_4 fails to come down according to the above method since it is precipitated as the basic phosphate of these heavier metals and is dragged down by the flocculent $Fe(OH)_3$ and $Al(OH)_3$ precipitates. Therefore, when one or both of these metals were absent a solution of ferric ammonium sulphate sufficient to give .04 grams per sample was added and a flocculent $Fe(OH)_3$ precipitate formed. (2) In the removal of the manganese, the solution was made alkaline with NH_4OH and H_2S gas was introduced instead of the addition of $(NH_4)_2S$ as called for in the above method. This method is quantitative in all respects but requires considerable time to make each determination because it is necessary for the manganese, aluminum and iron to be removed before the calcium can be quantitatively determined. As these elements were removed, the weight of precipitate deposited on the filter paper was estimated for each element which made it possible to make a rough comparison of the precipitate of each element with those of the various layers in the soils of the habitats. These comparisons confirmed the early quantitative measurements in so far that they were low and irregular. In 13 soil solutions there was not sufficient soluble iron (ferric form) to precipitate out the phosphorous and it was necessary to add this element. This fact points to a definite ferric iron deficiency in the soils of the region.

Determination of the Hydrogen Ion Concentration

The hydrogen ion concentration was determined by the quinhydrone method. It was practically impossible to make colorimetric determinations because of the highly colored water extracts due to the presence of considerable organic matter in the various layers of the first foot of soil. Two determinations were made of each sample, and in most cases these determinations were made independently by two different individuals.

Determinations of the Specific Electrical Conductivity

The specific electrical conductivity was determined by the methods and formulae given in practically all texts relating to chemistry. This measurement is a direct measurement of the ionic concentration of the solutions. The solutions may, however, differ widely in their specific electrical conductivities values, because of the presence or absence of certain ions of high velocities. In the present investigation the preliminary analytical determinations of the soil showed that the high and low velocity ions were approximately equal; therefore, the specific electrical conductivity values should afford a reliable

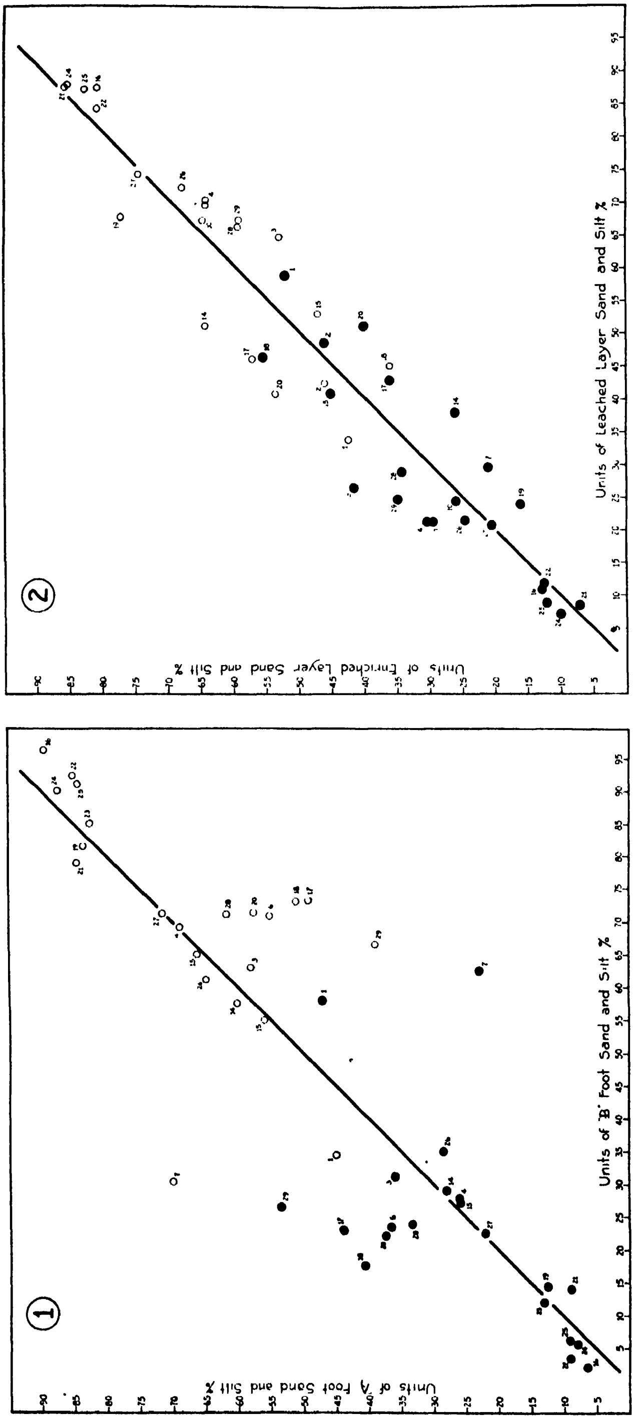

FIG. 6. A comparison of the results of the mechanical analyses of the soils listed in the tables. The solid dots represent the silt values and the open circles the sand values.

criterion of the ionic concentration of the soil extracts. As stated above, this method offered the most reliable measurement for total ionic differences where such small values were correlated with each element present in the soil.

Results

All of the data relative to the determinations which require statistical consideration are assembled in two special forms for presentation and discussion. The first is a series of tables which represent all the values and means relative to the divisions of the soil profile as outlined in the method

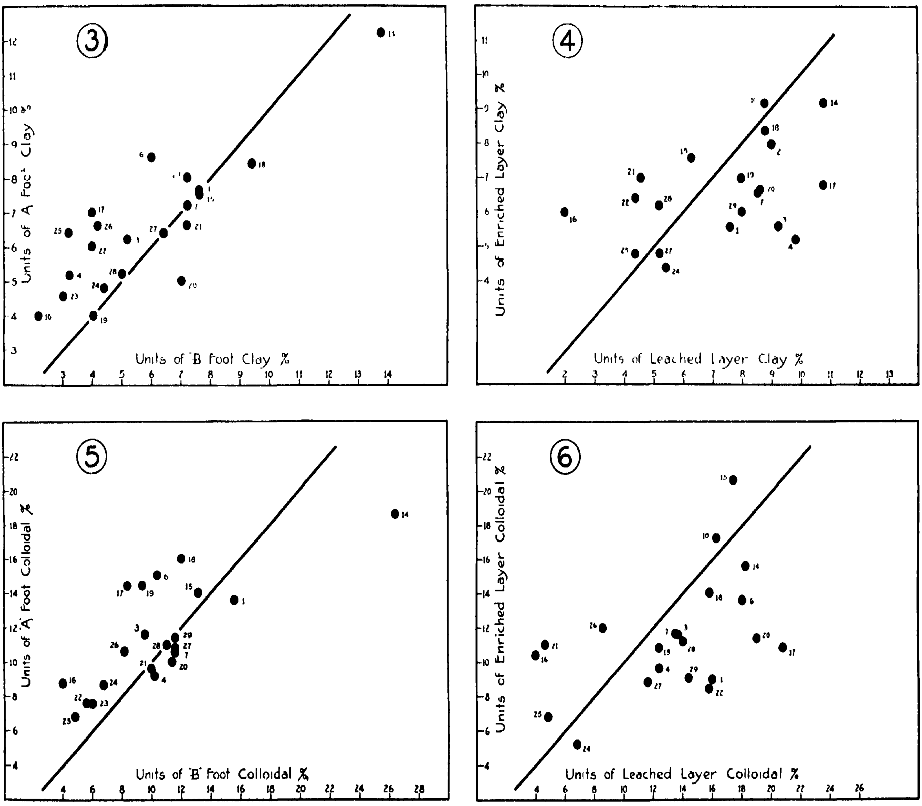

Fig. 7. A comparison of the results of the values from the mechanical analyses of the soils listed in the tables.

of obtaining soil samples. This form gives the analytical history of each individual soil sample as well as each individual unit of the profile. A particular division of the profile can be followed through showing its relationship to other profile measures for comparisons. The second form is a representation of the data in a series of graphs. This enables one to obtain a general picture of the relationships that exist between the various profile units at a glance. This is made possible by comparison of individual divisions associated as pairs

as established with an equality line. In these graphs representing the results of paired units of soil in the same profile, the values are represented on the axes of the ordinate and abscissa. When evaluating these data, differences can be observed when we consider that equal values or values essentially identical occur when all points representing each unit fall on the equality line or straight line (having a slope of 45° when the scales employed for the axis of the abscissae and ordinates are identical) representing the qualities of the values on the two scales. If differences in value occur between two units (such as the paired leached and enriched layers) then the points representing the values on the two scales will be distributed above and below the equality line according to their differences. The position of each solid dot and station number represents the value of a paired unit of analytical or physical measurements made in a single soil profile. In the diagrams the soil units are represented either numerically as to depth or by the specific name for each unit.

Mechanical Analysis

The results of the mechanical analysis of the soil are given in tables I and II and figures 6 and 7. In these diagrams only those soil profiles which have distinct enriched and leached layers in the first foot level are included for comparison of the paired measurements. The mechanical measurements as a whole show that the soil of the Cranberry Lake region is predominantly sand with a very low percentage of clay.

The mean values in table II indicate that the soils in the various habitats as well as the divisions of each profile are quite homogeneous. This is not true, however, when a comparison is made between the individual profile values in the 6 diagrams of figures 6 and 7 where these data indicate a high degree of heterogeneity. Although these two comparisons seem to contradict each other, each is nevertheless a reliable criterion of a special phase of comparison. The trustworthiness of these two types of measurement becomes clear as the following data are discussed. When we compare the sand (1.0–0.05 mm.), silt (0.05–0.005 mm.), clay (0.005–000), finer clay [7] (0.002–000 mm.), and colloidal mean values, it becomes very clear that only small differences exist between the sand, silt, clay and fine clay values of the enriched and leached layers, but the colloidal values are approximately 2 per cent higher in the leached layer. In the first foot level the sand value is approximately 4 per cent less; the silt value 3 per cent more; and the clays and colloidal values approximately 1 per cent more as compared with the values for the same fractions in the second foot level. These differences should appear very small when we recall that the humus layer is always a portion of the surface foot which would reduce in most cases the sand value and increase the other soil fractional values. Summarizing the mean mechanical values, it is

[7] The finer clay fraction values are very small and the accuracy of this measurement is questioned. Therefore, individual values of this fraction will not be treated in the discussion.

TABLE I. *Chemical and physical soil data for the habitats studied in the Cranberry Lake quadrangle*

Station No.	Soil profile divisions	pH	$K \times 10^{-6}$	Ca ppm.	Other ele-ments	Mechanical analysis percentages				
						Sand	Silt	Clay	Fine Clay	Col-loidal
1	A[1]	4.1	141	215.7	FeAl	45.4	47.0	7.6	6.2	13.6
Typical hard.-soft.[2] virgin forest	B	4.4	51	228.2	FeAl	34.4	58.0	7.6	6.8	15.6
	Humus 2–5[3]	3.3	539	258.6	Fe					
	Enriched 1–3	3.6	176	171.5	FeMn	42.4	52.0	5.6	5.6	9.0
	Leached 2	4.0	95	221.1	FeMn	33.6	58.8	7.6	5.6	16.0
2	Humus 1–6	4.3	565	187.4	FeMn					
Hard.-soft. virgin forest	Humus 6–14	4.6	480	132.0	FeMn					
	Enriched 1–3	4.1	140	164.3	FeMn	46.0	46.0	8.0	6.4	15.0
	Leached 1–2	5.5	45	109.0	FeMn	42.4	48.6	9.0	6.4	18.6
3	A	4.7	139	97.6	FeMn	58.0	35.8	6.2	5.2	11.6
Hard.-soft. virgin forest	B	5.2	62	88.5	None	62.8	32.0	5.2	3.2	9.6
	Humus 2–3	3.8	674	229.7	FeMn					
	Enriched .5	4.3	174	82.4	Mn	52.8	41.6	5.6	2.2	11.6
	Leached 1–2	4.2	88	71.3	None	64.4	26.4	9.2	7.2	13.6
4	A	4.6	254	231.4	FeMn	68.8	26.0	5.2	5.2	9.2
Hard.-soft. virgin forest island	B	4.7	73	216.5	FeMn	68.8	28.0	3.2	3.2	10.2
	Humus 6	3.5	842	255.8	Fe					
	Enriched 2	4.5	170	204.0	FeAlMn	64.4	30.4	5.2	5.2	9.6
	Leached 1–4	4.5	111	212.6	FeMn	70.0	21.4	9.8	4.4	12.4
5	Humus 1	4.1	496							
Pure softwood	Soil 1.5	4.3	365			67.2	24.8	8.0	5.0	10.8
6	A	4.6	75	200.4	FeMn	55.0	36.4	8.6	6.0	15.0
Beech birch forest	B	4.9	52	149.3	FeMn	70.6	23.4	6.0	5.6	10.4
	Humus 1–2	4.1	922	241.0	FeMn					
	Enriched 1–2	4.5	159			52.0	40.4	7.6	6.0	13.6
	Leached 1–2	4.2	84			57.0	31.4	11.6	9.6	18.0
7	A	4.0	138	162.0	FeMn	70.0	22.8	7.2	6.2	10.6
Hard.-soft. forest	B	4.9	74	170.0	FeMn	30.4	62.4	7.2	3.8	11.6
	Humus 1–4	3.3	446	174.8	FeMn					
	Enriched .5–1	4.6	162	79.7	FeMn	64.0	29.4	6.6	5.4	11.6
	Leached 1–2	4.9	96	70.0	None	70.0	21.4	8.6	6.2	13.6
8	Organic M 1	4.2	724	114.4	FeMn					
Hard.-soft swamp forest	" M 2–6	4.6	582	116.9	Mn					
	" M 6–14	5.6	62	89.0	Mn					
	" M 14–25	5.7	55	84.4	FeMn					
9	A "organic"	5.0	722	284.3	FeAlMn					
Black ash community	Humus 4	5.1	794	393.7	FeAlMn					
	12–18 hardpan	5.5	169	150.1	FeAlMn	46.4	35.0	18.6	15.2	29.6
	18–24 "	5.7	162	91.8	FeAlMn	38.0	48.8	13.2	10.2	22.6

[1] A = 1st foot, B = 2nd foot.
[2] Hard. = Hardwood, Soft. = Softwood. For full designation of the various stations see earlier pages.
[3] Thickness in inches.

TABLE I. (*Continued*)

Station No.	Soil profile divisions	pH	K × 10⁻⁶	Ca ppm.	Other elements	Mechanical analysis percentages				
						Sand	Silt	Clay	Fine Clay	Colloidal
10 Old white pine forest	Humus 1-6	3.8	706	233.8	FeAlMn					
	" 6-12	4.0	553	193.3	FeMn					
	" 12-18	3.7	968	212.0	FeAlMn					
	" 18-26	3.6	698	197.4	FeMn					
	Enriched 2-4	3.7	144	209.8	FeMn	64.8	26.0	9.2	5.2	17.2
	Leached 2	4.0	78	186.5	FeMn	66.8	24.2	8.8	7.2	16.2
	Hardpan 1-5	4.9	88	103.0	FeAlMn	68.8	23.0	8.2	4.2	12.2
	Inorganic soil below humus 1-24					65.6	25.0	9.4	12.4	13.3
11 Bog veg.	Organic M 2	3.4	490	71.	Mn					
	" 2 8	3.4	383							
	" 8-14	4.0	138							
	" 14 26	5.0	113	114.6	FeMn					
	" 26-28	5.0	181	118.3						
12 Tamarack bog	Organic M 1-2	3.9	386	96.4	FeMn					
	" 2-8	4.2	611							
	" 8-14	4.2	469							
	" 14-26	5.1	278							
	" 26 38	5.4	212	128.3	Mn					
13 Tamarack bog	Organic 1-2	4.1	402	121.5	Fe					
	" 2-8	4.5	648							
	" 8-14	4.6	518							
	" 14-26	5.7	268							
	" 26-38	5.2	274	124.3	FeMn					
14 Young white pine	A	4.6	90	79.5	FeMn	60.0	27.8	12.2	7.6	18.6
	B	5.5	40	67.3	Fe	57.4	28.8	13.8	9.2	26.4
	Humus 4	3.9	410	98.7	FeMn					
	Enriched .75	4.7	98	192.3	FeMn	64.4	26.4	9.2	7.6	15.6
	Leached 2-3	5.0	86	129.5	FeMn	50.8	38.4	10.8	6.8	18.2
	Inorganic soil 5-24					65.6	27.0	7.4	13.6	12.4
15 Young white pine	A	5.5	78	82.6	FeMn	66.0	26.4	7.6	7.4	14.0
	B	5.8	68	64.1	FeMn	64.8	27.6	7.6	6.8	13.2
	Humus 4	4.2	399	112.7	FeMn					
	Enriched .75	4.6	78	122.4	FeMn	47.0	45.4	7.6	10.5	20.6
	Leached 2-3	4.8	54	90.4	FeMn	52.8	40.9	6.3	8.4	17.4
16 Hardwood climax forest	A	5.2	66			89.6	6.4	4.0	2.0	8.8
	B	5.4	28			96.0	2.0	2.0	3.0	4.0
	Humus .75-1	4.1	797							
	Enriched 2	4.5	130			81.2	12.8	6.0	2.6	10.4
	Leached 1-2	4.7	93			87.0	11.0	2.0	2.2	4.0
17 Bunchberry community	A	4.2	117			49.2	43.8	7.0	6.0	14.4
	B	4.7	53			73.2	22.8	4.0	2.0	8.4
	Humus 3	3.6	165							
	Enriched 1-2	3.9	121			57.2	36.0	6.8	6.4	10.8
	Leached 1-2	4.8	94			46.2	43.0	10.8	8.4	20.8

TABLE I. (*Continued*)

Station No.	Soil profile divisions	pH	K × 10⁻⁶	Ca ppm.	Other elements	Mechanical analysis percentages: Sand	Silt	Clay	Fine Clay	Colloidal
18 Young yellow birch	A	5.0	108	100.8	FeMn	51.0	40.6	8.4	7.6	16.0
	B	5.2	53	124.9	FeMn	73.0	17.6	9.4	6.6	12.0
	Humus thin	5.1	300	126.4	FeMn					
	Enriched ind.[4]	4.5	103	81.0	FeMn	36.0	55.6	8.4	5.6	14.0
	Leached "	5.5	45	84.3	FeMn	44.8	46.4	8.8	6.8	15.8
19 Mixed hardwoods	A	5.9	40	138.1	FeMn	83.6	12.4	4.0	4.2	14.4
	B	5.1	61	160.5	Mn	81.6	14.4	4.0	3.6	9.4
	Humus thin	5.5	439	142.0	FeMn					
	Enriched ind.	5.1	61	112.4	FeMn	77.2	15.8	7.0	3.6	10.8
	Leached "	5.2	70	117.3	FeMn	67.6	24.4	8.0	5.0	12.4
20 Young aspen	A	5.0	70	112.6	FeMn	57.6	37.4	5.0	3.0	10.0
	B	5.2	54	79.0	Mn	71.2	21.8	7.0	5.0	11.4
	Humus thin	4.5	1054	194.6	FeMn					
	Enriched ind.	4.8	133	94.1	FeMn	53.6	39.8	6.6	3.8	11.4
	Leached "	4.8	98	80.4	FeMn	40.6	50.8	8.6	7.6	19.0
21 White clover community	A	5.5	60	78.4	FeMn	84.4	9.0	6.6	4.2	9.6
	B	5.7	51	67.8	FeMn	79.0	13.8	7.2	4.6	10.0
	Humus 1 2	5.2	1686	117.	FeAlMn					
	Enriched 1–3	5.4	68	68.1	FeMn	86.0	7.0	7.0	3.2	11.0
	Leached 1	5.6	41	69.3	FeMn	87.0	8.4	4.6	2.6	4.6
22 Scrubby soft.-hard.	A	5.5	84	87.4	FeAlMn	85.0	9.0	6.0	4.6	7.6
	B hardpan	5.9	41	79.0	FeAlMn	92.4	3.6	4.0	4.0	5.6
	Humus 1–2	6.2	272	132.1	FeAlMn					
	Enriched 3–16	5.5	106	72.9	FeAlMn	81.2	12.4	6.4	5.2	10.8
	Leached 4	5.7	47	74.4	FeAlMn	83.6	12.0	4.4	2.8	8.4
	Hardpan layer	5.5	33	68.4	FeAlMn	93.6	2.0	4.4	2.0	15.8
23 Scrubby soft.-hard.	A	4.3	80	73.0	FeAlMn	82.4	13.0	4.6	4.6	7.6
	B hardpan	4.8	38	76.4	FeAlMn	85.0	12.0	3.0	1.6	6.0
	Humus 1–2	4.6	304	70.8	FeMn					
	Enriched 1–2	4.3	61	69.4	FeAlMn	77.0	17.4	5.6	3.6	8.0
	Leached 2–4	4.8	47	71.8	FeMn					
24 Shrub and herb community	A	4.9	88	71.3	FeAlMn	87.4	7.8	4.8	3.8	8.6
	B hardpan	5.1	47	60.4	FeAlMn	90.2	5.4	4.4	2.4	6.8
	Humus 1–2	4.5	240							
	Enriched 1–2	4.7	77	81.2	FeAlMn	85.6	10.0	4.4	3.4	8.4
	Leached 2–3	5.2	46	56.4	FeAlMn	87.4	7.2	5.4	4.4	6.8
25 Shrub and herb community	A	5.6	59	64.7	FeAlMn	84.4	9.2	6.4	4.0	6.8
	B hardpan	5.7	41	64.8	FeAlMn	90.8	6.0	3.2	3.2	4.8
	Humus 1–2	5.2	970	92.1	FeMn					
	Enriched 1–14	5.4	67	84.5	FeMn	83.2	12.0	4.8	3.2	6.8
	Leached 2–4	5.6	42	60.7	FeAlMn	86.8	8.8	4.4	3.4	6.8
26 White pine-shrub	A	5.1	77	70.3	Fe	64.8	28.6	6.6	5.0	10.6
	B	5.5	46	62.2	Fe	60.8	35.0	4.2	3.6	8.2
	Humus—soddy	5.2	146	79.7	Fe					
	Enriched thin	4.9	78	76.9	FeMn	68.0	24.0	8.0	6.0	12.0
	Leached "	5.1	59	68.8	Fe	72.0	22.6	5.4	4.4	8.6

[4] Ind. = Indefinite thickness.

TABLE I. (*Continued*)

Station No.	Soil profile divisions	pH	K × 10⁻⁶	Ca ppm.	Other elements	Mechanical analysis percentages				
						Sand	Silt	Clay	Fine Clay	Colloidal
27 White pine-shrub	A	4.9	68	68.	FeMn	71.6	22.0	6.4	5.0	10.8
	B	5.3	28	54.9	Mn	71.0	22.6	6.4	4.4	11.6
	Humus soddy	4.9	159	86.3	FeMn					
	Enriched thin	5.4	76	80.0	FeMn	74.8	20.4	4.8	4.4	8.8
	Leached thin	5.5	59	59.2	Mn	74.0	20.8	5.2	5.6	11.6
28 Hawkweed retrogression area	A	5.5	81	61.2	FeMn	61.6	33.2	5.2	5.2	11.0
	B	5.3	28	58.0	FeMn	71.2	23.8	5.0	4.0	11.0
	Humus 1–2	5.2	167	80.	FeMn					
	Enriched 1–2	5.0	91	72.0	FeMn	59.4	34.4	6.2	4.2	11.2
	Leached 1	5.2	45	73.0	FeMn	66.0	28.8	5.2	3.6	14.0
29 Moss retrogression area	A	5.4	75	64.3	FeMn	38.8	53.2	8.0	6.0	11.4
	B	5.2	33	60.0	FeMn	66.4	26.4	7.2	6.2	11.6
	Humus 1–2	5.1	154	68.3	FeMn					
	Enriched 1–2	5.3	100	71.4	FeMn	59.2	34.8	6.0	4.0	9.0
	Leached 1	5.3	39	54.3	Mn	67.2	24.8	8.0	5.0	14.4

TABLE II. *Mean values of the chemical and physical soil measurements listed in diagrams of figures 6–10*

Profile division	pH	K × 10⁻⁶	Mechanical analysis percentages				
			Sand	Silt	Clay	Fine clay	Colloidal
A	4.96	140	66.89	26.09	6.56	5.19	11.44
B	5.22	74	70.54	23.13	5.87	4.42	10.37
Humus	4.10	530					
Enriched	4.68	107	64.02	29.41	6.57	5.22	11.36
Leached	5.01	69	64.45	28.35	7.27	5.90	13.24

perfectly obvious that they are important in so far as they point out the general physical composition of the soil in the region and form the nucleus from which the deviations of the various measurements of the profile divisions can be determined.

All the paired values of the mechanical analyses are listed in figures 6 and 7, but in diagrams 1 and 2 are included two sets of paired values because the sand and silt measurements show correlation and for space reasons can be adequately grouped together for comparison. The open circles represent the paired sand values while the solid dots represent the paired silt values.

A comparison of the sand, silt, clay and colloidal values of the various divisions of the individual profiles in the diagrams show that the dots are quite uniformly distributed for some distance along both sides of the equality line. Such a distribution clearly shows what a wide range of differentiation exists between the values of the various profiles, but the differentiation in

most cases between the values of the various divisions of an individual profile are not large.

Space is not available for treatment of each individual case (which is also true for the analytical and electrometric determinations), but a discussion of a few measurements seems necessary to emphasize the heterogeneous composition of the soil in the various habitats. A comparison of the sand values of the first foot levels between stations 24 (sand ridge habitat) and 6 (beech-yellow birch habitat) shows the former value is 87.4 and the latter 55.0 per cent. Correspondingly large differences also exist between the other divisions of the profiles, but only small differences occur between the various divisions of each profile. As previously stated, the sand and silt measurements show correlations, since a high sand value is always associated with a low silt value, which is likewise true of the colloidal content, while the clay value in practically all cases is very low. Another interesting comparison is between the sand values of the first and second foot levels of stations 16 (climax hardwood) and 1 (typical virgin hardwood-softwood), the former values are 89.6 and 96.0 per cent, while those of the latter are 45.4 and 34.4 per cent. An inspection of the mechanical measurements of the enriched and leached layers of station 10 (old white pine) show that they closely parallel those of station 14, a habitat supporting a fine stand of young white pine. No comparison could be made between the first foot levels of these two stations because the humus layer of station 10 is 26 inches deep, but the first 12 inches of inorganic soil below the humus of the two profiles shows a high degree of parallelism. All of these measurements indicate that the soils supporting these pure white pine stands are considerably higher in silt, clay and colloidal content than the habitats which do not carry white pine. This phase of the investigation will later be discussed in more detail. The mechanical measurements of stations 22–25 (sand ridge habitats) as would be expected, show an extremely high percentage of sand and the second foot values are higher in every case than those of the first foot level.

Returning to the consideration of individual differences between divisions of a single profile, it is apparent that rather large differences prevail between the soil fractions of the first and second foot levels of stations 6, 17, 18, 20 and 29. Differences also appear between the enriched and leached layers of these stations but are greatly reduced as compared to those of the first and second foot levels. These data as well as those cited above confirm the statement previously made that the soil as a whole is predominantly sand, but due to the manner of deposition during and after the period of glaciation a state of heterogeneity is now apparent. Because of the high percentage of sand in several of the habitats, which is correlated with an open structure, the leaching out of considerable amounts of desirable nutrient elements could occur more rapidly than in a compact soil. The results of the following analytical determinations will throw some light upon this subject.

Water Soluble Calcium, Manganese, Aluminum and Iron

The results of the calcium, manganese, aluminum and iron determinations are given in table I. For reasons stated previously, quantitative determinations were made for calcium and qualitative (in part) for the other elements listed above. The measurements are significant as a whole because they reveal the low and irregular amounts dissolved in the soil solution. Iron was absent in 13 soil samples, manganese in 10 samples, while phosphorous was present in all cases. Calcium was present in all of the soil samples, but ranged from 54.3 to 393.7 parts per million. The former value represents the calcium content in the leached layer of station 29 (retrogression habitat), while the latter value is the calcium determination of the humus layer (4″ in depth) of station 9, which supports a dominant stand of black ash. The calcium content is irregularly distributed both as to depth and layers of the soil profiles. The calcium values of the leached layers are higher than those of the enriched layers in stations 1, 4, 18, 19, 21, 22, 23, 28. In stations 1, 7, 18 and 19 (virgin forest) the calcium measurements are higher in the second foot level than those of the first foot level, while in stations 28 and 29 (retrogression habitats) the calcium measurements are practically equal. With the exception of stations 14, 15, 19, 23 and 29, the calcium values of the humus cover are consistently higher than those of the inorganic divisions in each profile. The humus layers of station 10 (old white pine) are remarkably high in calcium as compared with equal depths of organic deposits in stations 8, 11, 12 and 13 supporting swamp and bog types of forest vegetation. Other comparisons become equally interesting when the calcium values of the hardwood and hardwood-softwood climax forest soils are compared with the calcium measurements of the bog, swamp, fire and sand ridge habitats. The values of the former group are as a whole considerably higher than those of the latter which also show considerable variation. These data like many of the other soil measurements indicate that the climax virgin forest habitats as a group are more abundantly supplied with the soil constituents than those habitats which do not support the highest type of forest vegetation. The outstanding result of the calcium determinations is the fact that the humus contains very large amounts as compared with the other layers of the soil. These data demonstrate the ability of plants to take up for their metabolic processes an element sparingly distributed in the soil and to return the element to the soil in their organic deposition.

Aluminum, as stated above, is very low in quantity and limited in distribution, but wherever it is found in combination with calcium, manganese, and iron in the inorganic soil, a hardpan is also present. Aluminum was found in the humus covers only of station 1 (hardwood-softwood climax forest), and 21 (white clover), therefore the hardpan was not present. At station 4 (virgin forest), aluminum was present in the enriched layer but absent from the humus cover. In the following stations aluminum was present in the

humus layer and one or more of the inorganic divisions of the substratum: 9, black ash grove; 10, old white pine area; 22–25, sand ridge habitats.

Before an attempt is made to theorize concerning the chemical reactions responsible for the formation of the hard pan layers in certain localities of the Cranberry Lake region, more analytical evidence must be obtained from field samples.

Hydrogen Ion Concentration

The results of determinations of the hydrogen ion concentration are given in tables I and II and in figures 8 and 9. In general, these results are very significant since they show that the soil of the Cranberry Lake region is very acid. Furthermore, these data clearly demonstrate the existence of extreme differences of pH values in the soil of the various habitats.

An inspection of the mean paired values [8] taken from the 4 diagrams of figures 8 and 9 show that the soil with the exception of the enriched layer becomes less acid with depth. These values also show that the humus layer (pH 4.10), is more acid than any of the other layers or divisions of the profile. The enriched layer (pH 4.68), is more acid than the leached layer (pH 5.01), while the second foot level (pH 5.21) is less acid than the first foot (pH 4.96), of the soil. These differences become more significant when we recall that H-ion values are not measured on an arithmetical but on a logarithmic scale. A further comparison of the mean humus values (not included in table II but determined from table I) is interesting when we note that stations 1–17 supporting hardwood and softwood-hardwood climax vegetation have a pH 3.98 as compared with pH 5.01 for the burned areas in stations 18–20 and pH 5.10 for stations 22–29 which include the sand ridge and retrogression habitats. The mean pH values of the other profile division show a similar parallelism, but they are not as pronounced as those just cited.

These data strongly indicate that the humus of the climax forest habitats becomes very acid with age and accumulation, since it is 10 times as acid as the humus cover of the burned habitats supporting a young hardwood forest. Furthermore, this type of humus is also 10 times as acid as the humus cover composed principally of herbaceous and shrub deposition in stations 22–29, which would suggest that the type of dominant species present in an area influences the acidity of the humus formed. In addition the humus cover of the climax forest is equally as acid as the surface 4 inches of organic deposits of the swamp (stations 8 and 9) and bog (stations 11–13) habitats notwithstanding the fact that sphagnum moss is present in each area.

From the above data it is very apparent that the mean pH values vary widely among the various habitats. The differences between pH values become more significant when individual comparisons are made in figures 8 and 9. As an illustration, we note in station 1 (typical virgin forest) that the pH values of the humus cover is 3.30 as compared with 5.50, the value

[8] pH values for statistical means must be converted into cH values which is the measure of hydrogen ions in relation to OH-ions present.

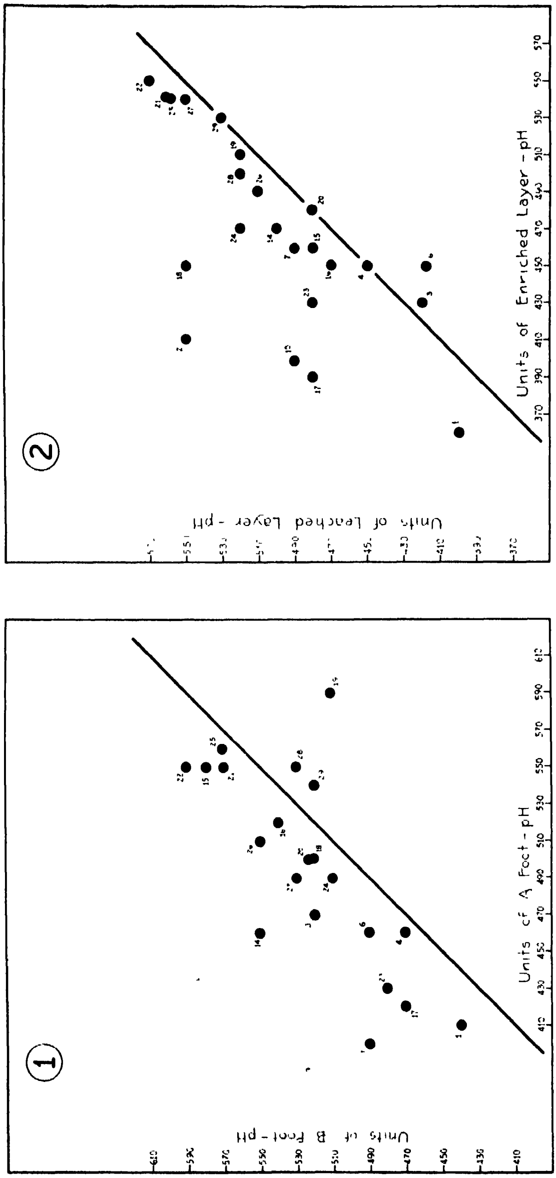

FIG. 8. A comparison of the hydrogen ion concentration of the soils at the different stations.

of the humus deposit in station 19 (old burned area), which means that the former is 100 times as acid as the latter. The distribution of the dots in diagram 1 of figure 8 show that only 3 first foot layers are less acid than their associated second foot layer pairs, which confirms the mean data that the first foot level as a whole is more acid than the second foot level. A comparison of the hydrogen ion concentration between the leached and enriched layers in diagram 2 shows that the former are less acid in every case except 5, while 3

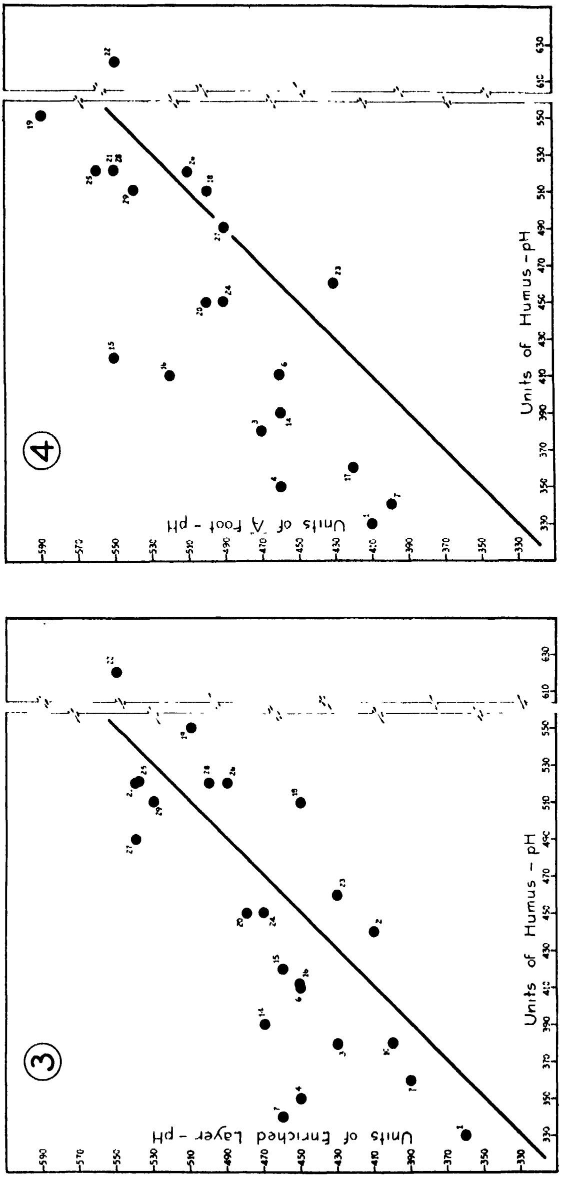

Fig. 9. A comparison of the hydrogen ion concentration of the soils at the different stations.

of these are equal to its associate pair, since they lie on the equality line. When individual profile pair values are compared, the enriched layer is often 10 times as acid as the leached layer which is a remarkable differentiation when we recall that the two layers are in close contact with each other. A comparison of the H-ion values in diagram 3, between the humus and enriched layers indicate a wide range of variation in the region as a whole. In the past, the general belief has been that the humus of forest soils is considerably

more acid than other layers or divisions in the profile. According to the measurements shown in figures 8 and 9, this is true only in part because of the 23 cases considered 7 enriched layers are more acid than their associated humus pairs. As a whole, there is approximately the same differentiation in the values between the humus and enriched pairs of the profiles of pairs as appears between the leached and enriched layers. Another interesting comparison is that of the pH values of the humus content of the first foot layers with the pH values of the total first foot layers in diagram 4. This comparison shows that the humus in most cases is more acid than the combined units of high acidity which comprises the general soil composite.

Summarizing the H-ion results, not only do large differences occur between the soil values of different habitats, but they also exist between the various layers and divisions of each profile of a single habitat. This condition brings forcibly to our minds the adjustment or adaptation the plants must make during their early periods of growth, as their roots enter and possibly feed in the various layers of the soil. The high acidity of the coarse needle (duff) humus in station 10, the old white pine habitat, is very significant and may play a very important rôle in retarding the natural reproduction in the area, because the seedlings may be unable to tolerate the severe hydrogen ion concentration during their early stages of development. Such an explanation may account for the absence of many herbaceous plants from certain areas which are common in other areas in the same region. Theorizing further, it is highly possible that certain buffers salts may be present in the humus or other layers of the soil profile, which have a stabilizing effect upon the chemical composition of the soil. It is also possible that certain plants which feed in these acid layers contain buffers in their cell sap able to reduce or modify the reaction of the high hydrogen ion concentration. This would seem to be suggestive in the case of *Trillium erectum, Dicentra cucullaria* and *Tiarella cordifolia*, since they apparently grow equally well in the extremely acid areas of Cranberry Lake region and the limestone soils of central New York.

The small amount of soluble calcium present in the various soil layers of the region appear to have little or no significances as to the degree of acidity the soil contains. This becomes apparent when we consider that among the various habitats which show a high percentage of calcium in the upper foot divisions only station 9 (black ash) shows a comparatively low hydrogen ion concentration in such layers. The fact that water runs freely through this habitat may be a more effective factor in the reduction of the acidity than the calcium content. The rôle of calcium in combination with other elements in the region may, however, be very important as a buffer to certain toxic substances associated with high acidity. This hypothesis becomes more realistic when we recall that aluminum apparently plays an important rôle in the formation of the hardpan layer in certain habitats. The writer in the near future hopes to throw some light upon the rôle of buffers in the soils of the region.

Specific Electrical Conductivity

A comparison of the specific electrical conductivity results in the 3 diagrams of figure 10 as well as in table I and II, show that not only do profound differences exist between the soil constituents of the various habitats but that the various layers and levels within a soil profile are heterogeneous to a remarkable degree. Except for the humus the K[9] values of the soils in the Cranberry Lake region as a whole are quite low as compared with areas elsewhere that are not high in sand. Before the K values are discussed in detail, it would be well to recall that the specific electrical conductivity measurements represent the total electrolytic concentration of the soil or its entire soluble chemical composition.

According to the soil measurements of table I, shown in the diagrams of figure 10, the specific electrical conductivity values of the humus layers are very high when compared with the other layers of the soil. Since the calcium data show that the humus layers are richer in this element than the other divisions of the soil profiles and as the nitrogen content is also higher we would naturally expect the K values as a whole to be consistently high. There is, however, a very wide range of differentiation between the values of the various habitats when individual cases are considered. For convenience, all of the humus K values of table I, which are not paired with associated enriched layer values in diagram 3 of figure 10, will be discussed during the treatment of the paired values of diagram 1 of the first and second foot layers of the substratum. Furthermore, other data relative to the K values of the humus which can be more clearly explained by comparison with the data of the first foot of soil will also be introduced.

When we compare the values of each pair of layers (humus and enriched) in diagram 3 the positions of the dots show that in every instance the K values of the humus layers are considerably higher than the values of the associated enriched layers. With the exception of three stations, 20, 21 and 25, all of the high K values of the humus layers are confined to stations 1, 2, 3, 4, 6, 7 and 16 which support either hardwood or hardwood-softwood climax forest communities, and their associated pairs are the highest K values of all the measurements of the enriched layers. These data strongly indicate that old, well developed humus layers influence the richness of soil constituents in the enriched layers. In order to understand clearly why the K values are so high in the humus layers of stations 20, 21 and 25, it would be well to recall the descriptive details concerning their plant covers. Station 20 is a burned area now supporting a heavy stand of dominant young aspen which adds considerable leaf litter to the soil each year. The humus layer is very thin but well decomposed and the high K values should indicate that considerable soil constituents are included in the leaf composition which readily becomes soluble. This is confirmed in part by the large calcium results. The humus layer of station 21, where white clover is abundant, represents the highest humus K

[9] K, as here used, is the common symbol for specific electrical conductivity.

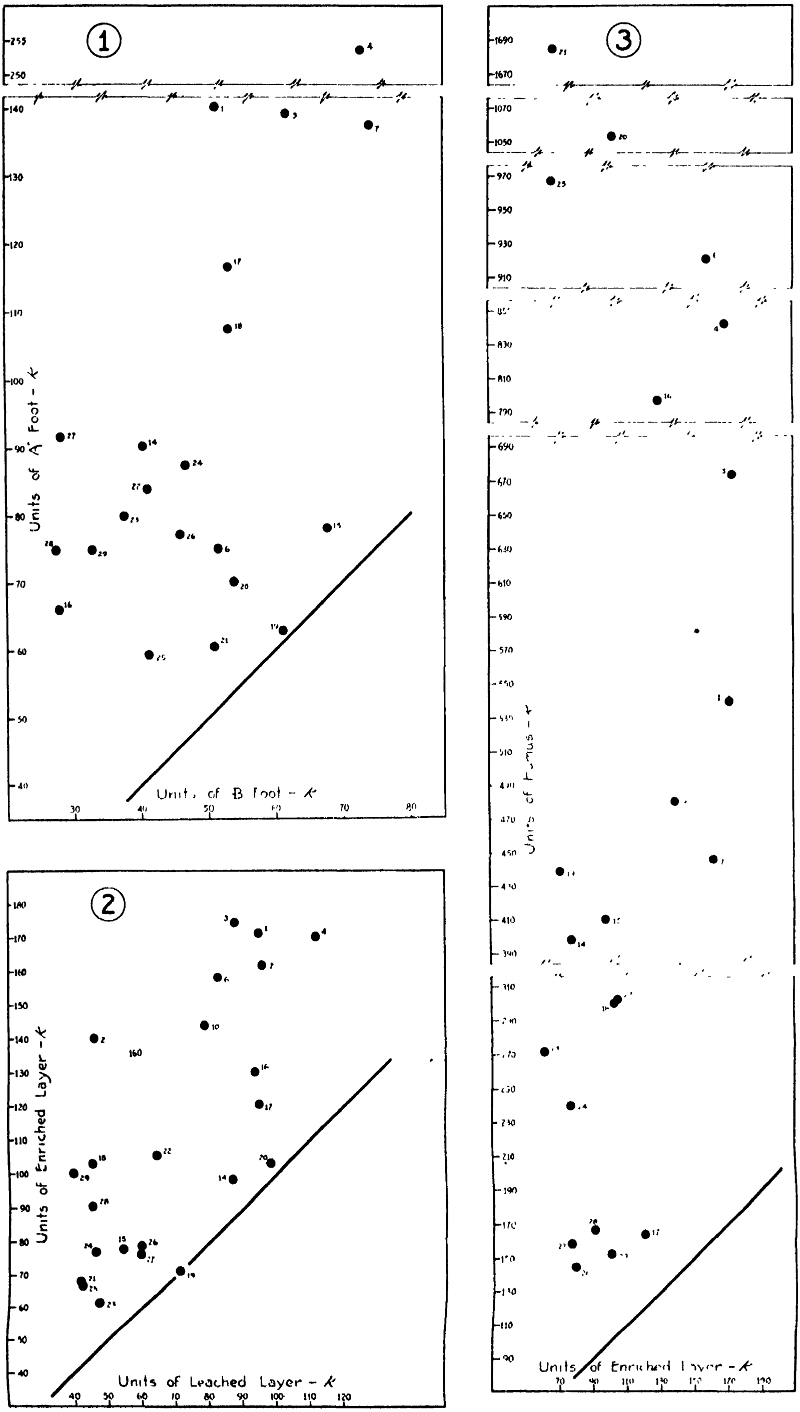

Fig. 10. A comparison of the electrical conductivity (K × 10^{-6}) values in the soils at the different stations.

value (K 1686) of all the habitats. This may be attributed to an increase of nitrogen since the calcium, manganese and iron measurements are quite low as compared with those of several other habitats. In addition, the K values of the soil layers directly below the humus (the approximate depth that the clover roots extend into the soil) are quite low as compared with similar measurements in other habitats. The significance of the K measurements of the humus in this habitat is the apparent ability of a domesticated plant to introduce a profound change in a forest soil which comes within the influence of its roots. The K values of the humus (K 165) and enriched (K 121) layers of station 17 which support a dense growth of *Cornus canadensis* are extremely low as compared with those of other habitats located in the hardwood-softwood and hardwood climax forest habitats. Since the roots of these plants do not extend below the enriched layer, it would indicate that the depth of the root system of certain plants plays an important rôle in the amount of soil constituents that a definite layer may contain. Furthermore, it is highly possible that dense stands of this species are better adapted to areas of less fertility than most of the areas within a virgin hardwood or hardwood-softwood region and concentrates community growth in such places. To offer an adequate explanation other than the heterogeneous composition of the soil for the high K value (K 968) of the humus layer and the very low K value (K 67) of the enriched layer in station 25, a sand ridge habitat supporting a thin ground cover of dwarfed shrubs and low growing herbaceous species, is very difficult; especially so in view of the fact that the K values of both the humus and enriched layers are very low in station 24 located within a few rods of station 25. These data are quite in harmony with results obtained in 1912 by Alway and Trumbull ('12) from humus and nitrogen determinations. They found that when 5 prairie soil samples were taken close together, differences in percentage of humus and nitrogen were as high as 15 per cent. When the samples were taken over a comparatively wide range, the differences increased to 30 per cent.

A comparison between the enriched and leached layers shows that the specific electrical conductivity values are much higher in the enriched layer. This is significant since it gives a quantitative justification of the names commonly applied to these layers. Of the 23 habitats considered, all values of the enriched layers are higher than those of their paired leached layers. One case, however, which occurs in station 19, the two values are practically identical. As stated elsewhere, this habitat was severely burned which may have had considerable influence upon the soil composition. Wide variations between the two layers within a soil profile are not uncommon, but it is interesting to note that the values of both the enriched and leached layers are quite high in both the virgin forest and the hardwood climax forest habitats as compared with habitats where burns and unusual topographic features are associated with the vegetation. A further study of the paired values show that the enriched layer of station 2, a habitat supporting a highly developed hard-

wood-softwood forest, is very high in soil constituents (K 140) as compared to the leached layer (K 45) which is extremely low. A similar difference, although the values are not as high, exists between the enriched (K 100) and leached (K 39) layers of station 29, a habitat now covered with moss, but where the original vegetation was destroyed by fire. These are certainly outstanding irregularities of individual differences within a habitat. Comparatively uniform values may occur within habitats and these habitats still may differ widely in their relative values as indicated by the values of stations 1 and 24. The value of the enriched layer of station 1, the most typical hardwood-softwood virgin forest in the region, is the highest for such a layer (K 176) analyzed during the present investigation and its associated pair, the leached layer, is also decidedly high (K 95), while the values of the enriched (K 77) and leached (K 46) layers of station 24 (sand ridge habitat) are extremely low. Such outstanding differences as cited would certainly indicate that the chemical composition of the soil in certain layers might account for differences in vegetation.

The positions of the solid dots in diagram 1 shows that in every instance the K values of the first foot are higher than those of the associated second foot soils, and in several cases the difference is conspicuously large while in one case (station 19, old burn habitat) it is very small.

A study of individual differences between the K values of the habitats show that quite consistently high values are associated with both the first and second foot levels of the soils in stations 1, 3, 4, and 7 supporting hardwood-softwood climax forest communities as compared to the low values in the soils of stations 6 and 16 supporting pure hardwood climax forest communities. A further comparison demonstrates that stations 18, 19, and 20 (burned areas) and stations 28–29 (retrogression habitats) have also low values as compared to the virgin hardwood-softwood forest habitats, and with the exception of stations 28–29, the K values are quite irregular. To offer an explanation for the distribution of these inconsistent K values, either from the standpoint of habitat location or type of vegetation supported by each, we must recall the descriptive details of each station or habitat involved. First, the heterogeneous composition of the soil seems the most logical explanation for the decidedly large differences between the K values of habitats 1, 3, 4, and 7 as a group as compared with those of habitats 6 and 16, since the climatic and topographic features are quite similar. Since habitats 6 and 16 support pure climax hardwood forest communities, and the mechanical analyses of the soils show large differences between the two habitats, the data naturally suggest that the chemical differences of the soil might be a major factor in determining such a distribution. The low K values of the burned habitats 18, 19, and 20 may in part be attributed to the thin humus layers which would be low in total nitrogen as compared to the deep humus layers of the virgin forest. Furthermore, it is highly possible that erosion and leaching has carried away considerable amounts of soil constituents following the destruction of the original humus

by fire before the ground cover of the new vegetation was sufficiently abundant to prevent physical disturbances. The absence of the leached layer in various spots in these habitats is certain evidence of the severity of the erosion. Although the calcium values are low in these soils, they are criteria of low K values only in so far as they would indicate the possibility of other ions decreasing in like proportion. Since these habitats supported a virgin forest before the destruction of their vegetation by fire, it would seem logical to assume that the soil composition was roughly similar to that of the virgin forest habitats. Therefore, the decreased amount of soil constituents noted in the K determinations is obviously associated with burn effects and suggests in a striking manner the chemical disturbances that may occur after a forest fire. Again it would seem reasonable to conclude that soil heterogeneity is responsible for the low and irregular specific electric conductivity values of habitats 22–27 (sand ridge area) since practically all the analytical determinations show low results. In addition, when the above values are compared with the high sand content, they indicate in a profound manner the reason why these habitats are supporting a type of vegetation characteristic of the sand plain areas in certain parts of the Adirondacks. The low and rather uniform values of habitats 28 and 29 become self-explanatory when we consider the severe physical changes that the areas have undergone because of logging and fires which were no doubt accompanied by excessive soil erosion and leaching, the principal factors responsible for the loss of large quanties of nutrient materials from the soils. These together with the loss of a large percentage of the microorganism would definitely change the original chemical composition of the soil. So complete has been the soil disturbance from these apparent causes that only a few of the more tolerant pioneer plants characteristic of burned areas have been able to obtain a foothold in these habitats and in the region as a whole. It is highly possible the region may never regain its original soil composition and support thereon a dense growth of dominant red spruce.

Several of the specific electrical conductivity values of the various stations listed in table I and on the diagrams, have not heretofore been discussed because the physical or chemical composition of the profiles are of such a nature that special consideration must be given to these cases.

Beginning with the K values of station 9 (black ash) it becomes apparent that the value (K 722) of the first foot layer is practically 3 times as large as the highest value for the same level (K 254) of station 4 recorded among the various habitats. This high value is no doubt partially contributed by the humus layer 4 inches in thickness with a K value of (K 794) and a calcium measurement of 393.7 ppm. The second foot value (K 165) which includes the average of the lower 6-inch levels is also very high. This value, together with the specific electrical conductivity measurement of the first foot confirms the large amounts of calcium, aluminum, manganese, and iron compared with those of the other habitats investigated. The mechanical analysis of the soil shows that more than 50 per cent of it is clay and silt. This would definitely

indicate that the upper 28 inches (depth sampled) is of alluvial origin, and, as a matter of fact, the running water which drains the higher areas still passes through the habitat. Therefore, it would seem logical to conclude that during the period of water deposition certain ions were also deposited in varying abundance which would account for the high values obtained in the soil of this habitat as compared to the soils of other habitats where alluvial soils are not present. In addition, these ions by means of chemical reaction with each other and with the soil, as stated elsewhere, no doubt formed the hardpan layer which brought about a water and chemical relationship necessary for the growth and later the dominance of the black ash community in a hardwood-softwood climax forest. Since a high degree of mortality exists among the mature trees, and the saplings are making extremely slow growths, it is highly possible that the continual deposition of the humus and water solutes are bringing about an undesirable soil condition for the maintenance of the ash community and it will in time be replaced by other tree species.

A comparison of the K values of the soils of stations 10 (old white pine) and 14 and 15 (young white pine) reveal not only that large differences occur between the various layers but that the values of the old white pine soil are conspicuously higher in every layer and division than those of the two young white pine areas. The same relationship is also true of the calcium, manganese and iron values. The high K and calcium values of the four 6-inch units of the humus layer in the old white pine soil are very significant because they upset the old theory that large accumulations of pine needle humus lose a high percentage of their chemical constituents during the long time involved in deposition, decomposition and leaching. The K and calcium values (K 706) and (Ca 233.8) of the first 6 inches of humus are decidedly high as compared with the humus (4 inches deep) values (K 410) and (Ca 98.7) of station 14, the pure young white pine habitat.

Returning to the mechanical analyses of the three white pine habitats, it is interesting to note that the colloidal percentage of the profiles of the old and young white pine stands are slightly higher as a whole than those of the hardwood and softwood-hardwood habitats. These differences suggest that white pine is adapted to a sandy soil of comparatively high colloidal content provided it is well drained. This would account for the many very small groups of old white pine growing in the well drained sandy soils along the ridges and foot-slopes and elevated localities in wet areas of the uncut lands of the Cranberry Lake region. Only one case was observed where an old white pine tree (200 years) did not grow under conditions just described. This particular tree is growing among red spruce and hemlock in a bottomland area where the fine alluvial substratum is not especially well drained. It is not uncommon to see many small white pines less than 6 feet high growing in old swamp and bog areas but they are apparently unable to develop beyond a certain size or age. On the other hand, it is highly possible that certain soil reactions due to erosion and plant succession are playing an important rôle in the supposedly increased

white pine reproduction now so evident in certain localities of the region. White pine reproduction suggests that a few areas northwest of Cranberry Lake Village may in the future support large trees since many saplings which now occupy the ridges and footslopes are making rapid and vigorous growth.

A comparison of the specific electrical conductivity results of the soils in stations 11, 12 and 13 of the bog area definitely indicates that chemical changes are associated with plant changes in the various stages of succession. All the K measurements in these stations are limited to organic soil samples which represent a definite gradient increase in age and decomposition with depth. Only a small difference is evident between the K values of the first two inches of the soils in the three stations, nevertheless the results are all quite high as compared to those of the lower soil units. A very large differentiation exists, however, between the K results of the second soil units (2–8 inches) of station 11, (center of bog) and stations 12 and 13, (zones of small and large tamarack) the value of the former is (K 383) and those of the latter are (K 611) and (K 648) respectively. The presence of considerable erosion sand in the undecomposed sphagnum of station 11, as compared to well decomposed spagnum and needle accumulation in habitats 12 and 13, would in part account for the low value. This same explanation is not adequate for the low value (K 138) of the third unit sample (6–14 inches) of station 11 as compared to those of stations 12 (K 469) and 13 (K 518), but since a large portion of the former layer occurs in a practically saturated condition, it is possible that considerable quantities of the soil solutes are carried in the water which is retained by the soil units of stations 12 and 13 located higher above the water table. This suggestion is strongly confirmed where the K values of the 5th soil unit (26–38 inches) in stations 12 and 13 taken in the water table show a considerable decrease as compared with the 3d soil unit some inches above the water level. The K values of the lower units (14–38 inches) in these stations show a profound decrease with depth which is not true of the lower units (12–26 inches) of the unsaturated organic deposition of the old white pine habitat. Here is no doubt a case where the activities of organisms are able to bring about certain physical and chemical changes in the soil not possible in a saturated substratum.

From the data of stations 11–13, it becomes definitely evident that the differences between the K values, water levels, deposition and decomposition of the soil are highly correlated with succession and each stage supports certain dominant species characteristic of the specific environment. Therefore, one can safely assume that a change in the edaphic factors of a habitat may introduce a new environment highly desirable for the growth of species heretofore not adapted to the habitat. Such a condition has apparently taken place in station 11 where white pine saplings are quite abundant. Here the deposition of erosion soil (mostly sand) in the upper 12 inches of the substratum has no doubt adjusted the physical composition of the organic matter to such an extent that the white pines have been able successfully to maintain growth

to the present time. This explanation becomes more logical when we note the absence of white pine in Esker bog (fig. 2) where erosion has not been active and no inorganic soil occurs in the upper foot of the substratum. Thus it is evident that succession plays a very important rôle in the change of the edaphic and vegetational composition of an area.

Summarizing the specific electrical conductivity data, it is clearly evident that the soil of the Cranberry Lake region is spotted in its chemical composition. A similar parallelism exists for the results of mechanical analysis. It is highly possible that similar conditions occur in the small and supposedly uniform areas of the region if we can assume that the natural soil is similar to agricultural soils. According to Harris ('13) agricultural areas show a high degree of soil heterogeneity in small and apparently uniform plots, which is the basic reason for differences in plant growth and crop yields. Later Harris ('26) again sharply focussed the attention of students upon the trustworthiness of his earlier study of soil heterogeneity by offering evidence that the chemical irregularities of soils influence the physiochemical properties of the leaf tissue fluids of certain cotton species. Since soil heterogeneity plays such an important rôle in plant growth in agricultural soils, and the data of the present investigation clearly indicates that soil heterogeneity determines the dominant species in the various habitats studied, it would seem logical to conclude that the occurrence of definite indicator species in the Cranberry Lake region out of their natural environment, is due to a high degree of soil heterogeneity within a small area. This assumption can only be verified, however, by considerable detailed investigation which may show that the physical and chemical composition of the soil determines the actual position of each plant in a habitat.

Conclusions

The climax forest of the Cranberry Lake region is a mixed hardwood-softwood type growing in a podolized soil. The vegetation as a whole is composed of pure and mixed communities which are separated in certain areas by rather sharp boundaries while in other areas by transitional zones.

The mechanical analyses of the soil show that the substratum is predominately sand with a low percentage of clay as well as a low colloidal content. Large differences occur, however, between the values of the soils of the various habitats which definitely indicate the heterogeneity of the substratum.

In certain habitats hardpan layers occur below the leached layers in the soil profiles which apparently influence the type of vegetation these areas can support. The analytical data show that aluminum is present where the hardpans occur, which would strongly indicate that this element plays a major rôle in the formation of such layers.

The rôle of plant succession in certain areas of the Cranberry Lake region is of primary importance in bringing about changes in both the physical and chemical composition of the soil.

The analytical data reveal that in most cases the elements necessary for plant growth are low and irregular in water soluble forms. Calcium, although low and irregular in distribution, is more abundant in the humus cover than in the other divisions of the soil profiles notwithstanding the fact that the humus layer is generally more acid than the other layers of the profiles. Nitrogen is unusually distributed in the soils of the various habitats but due to certain limiting factors previously discussed this element could not alone account for the major differences in plant distribution observed in the region as a whole. The hydrogen ion concentration of the soil is very high; however, large differences often occur between the various divisions of a single profile. The enriched layer is definitely more acid than the leached layer which shows that small portions of the inorganic substratum may be a storehouse for certain ions.

Concerning the rôle played by specific elements in determining plant distribution, a definite value cannot be applied although the high acidity of the soil is suggestive. A major result of the present investigation, however, is that the specific electrical conductivity values (a measurement of the total ionic concentration) confirm the preliminary chemical measurements. Both point to the irregular distribution of the soil constituents of the Cranberry Lake region and suggest that certain ions accumulate in localized areas or pockets. The data also definitely indicate that the soil of the virgin or climax forest habitats are in most cases richer in soil constituents than that of habitats supporting less highly developed vegetation.

The study of the physical, chemical and electrometric measurements of the Cranberry Lake soil shows that a high degree of heterogeneity prevails from habitat to habitat in the same relation that the vegetation varies in composition. These results parallel those obtained by Harris and co-workers from agricultural soils in so far as they show that soil heterogeneity is correlated with plant heterogeneity.

The writer wishes to acknowledge the valuable information and advice of Dr. W. L. Bray, Dean of the Graduate School of Syracuse University, in the present investigation whose first hand knowledge of the vegetation of Cranberry Lake area has been gained after years of contact with the ecological problems of the region. To Prof. H. F. A. Meier, College of Forestry, Syracuse University, he also extends thanks for his encouragement and many helpful suggestions.

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FOLIAR DIFFERENCES IN EIGHT DUNE AND CHAPARRAL SPECIES [1]

EDITH A. PURER

San Diego, California

The purpose of this paper [2] is to show the differences in water content and leaf thickness of eight species in two differing habitats in San Diego County, California. Two stations were chosen where the plants were found in widely differing habitats, namely, on the Silver Strand, a coastal sand spit, extending from Coronado south to Imperial Beach and on a chaparral area northeast of San Diego, fourteen miles inland from the former station and at an elevation of about 150 feet.

Data on the environmental conditions were collected weekly for a period of sixty-two consecutive weeks. Evaporation rates were obtained from Livingston black and white porous cup atmometers (fig. 1). The instruments were located as nearly as possible in an area where they would be subjected to the same environmental conditions as the species studied. The precipitation data were obtained from the United States Weather Bureau station at San Diego, situated about equidistant from the two stations. Soil temperatures (fig. 2) were taken weekly by means of maximum and minimum thermometers placed horizontally at a depth of 30 cm. in wooden boxes constructed so as to prevent circulation of air while at the same time permitting ready access to the instruments following approximately the methods of Toumey and Stickle ('25). Soil moisture was determined from samples taken at depths of ten, twenty, thirty, forty and sixty centimeters. The results are given in percentages of dry weight of the soil. The different soil horizons were so similar that the wilting coefficients are the averages from samples at all depths (table I).

The soil in the two areas differs considerably (see Wiggins, '29), that at the Silver Strand being made up of loose, incoherent, rather coarse sand, containing about ninety per cent quartz, a little feldspar, with basaltic material especially prominent.[3] This soil is poor in nutrient materials, for organic substances which may be left in the soil are rapidly decomposed, and, owing to the physical structure of sand, the rain water carries the humus particles

[1] The publication of this article out of the order of the receipt of the manuscript is made possible by funds other than those of the Ecological Society of America.

[2] Presented before the Ecological Society of America at its meeting of December 29, 1933.

[3] Soil analysis was obtained through the courtesy of the U. S. Bureau of Chemistry and Soils.

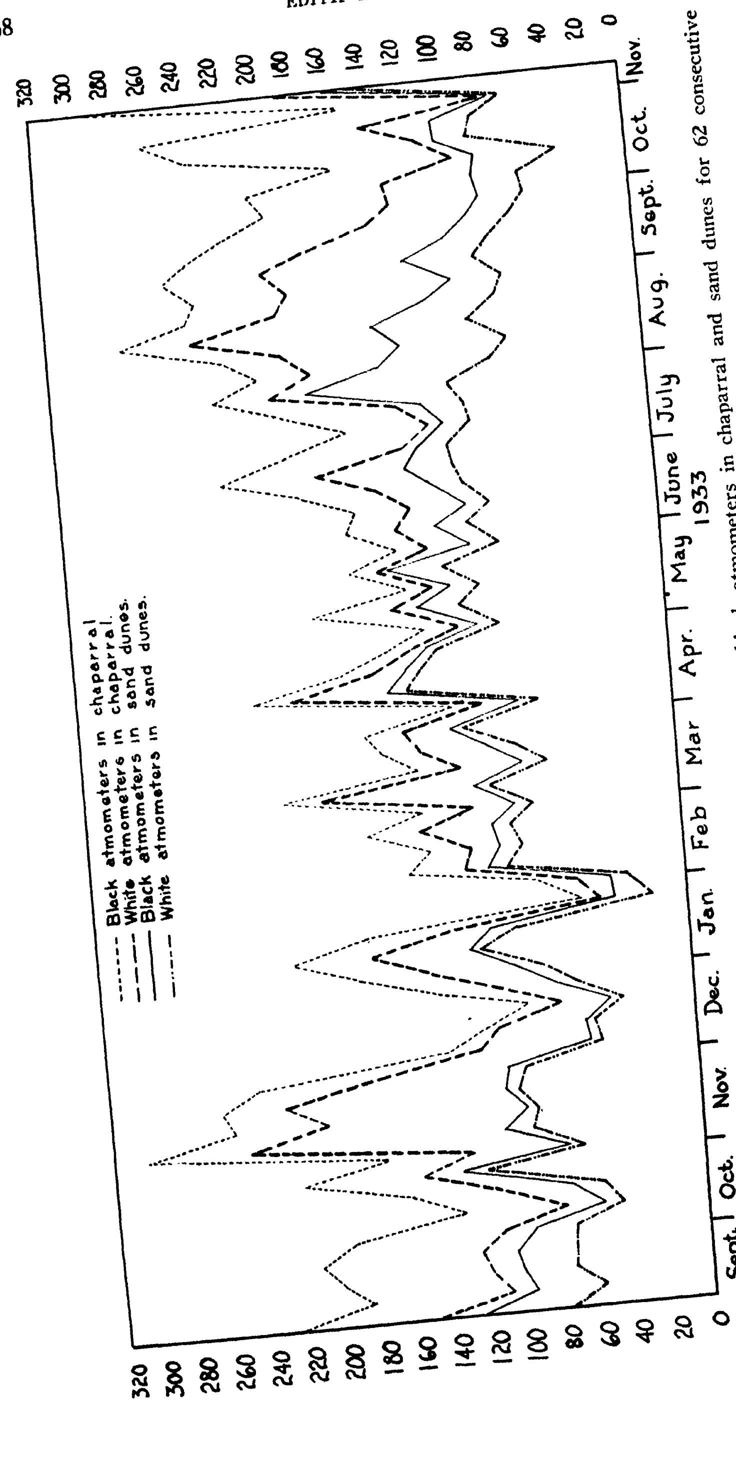

FIG. 1. Weekly evaporation rates in cubic centimeters from white and black atmometers in chaparral and sand dunes for 62 consecutive weeks.

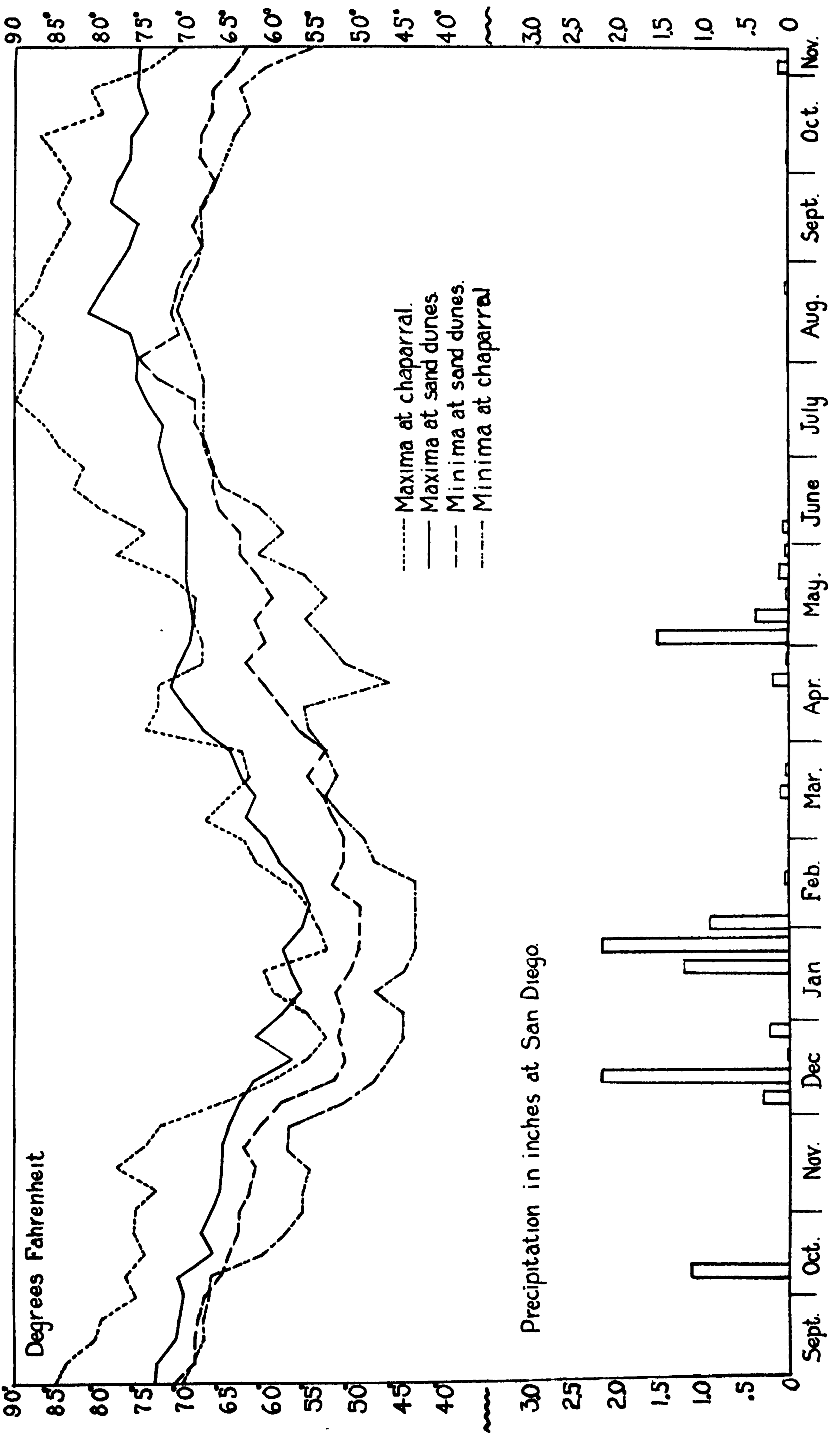

FIG. 2. Maximum and minimum soil temperatures in chaparral and sand dunes and precipitation for both areas for 62 consecutive weeks.

TABLE I. *Range of soil moisture, in percentages of dry weight, in the sand dunes and in the chaparral community. The sand has a wilting coefficient of 1.5 per cent, the soil of the chaparral one of 20.1 per cent approximately.*

	Sand dunes					Chaparral				
Depth in cm.	10	20	30	40	60	10	20	30	40	60
Date 1932–3										
Sept.	.4	.5	.6	.8	.8					
Oct.	1.4	3.9	2.6	1.1	.7					
Nov.	2.6	3.1	3.6	4.8	3.1					
Dec.	2.1	3.2	3.0	3.6	3.6					
Jan.	5.0	5.7	5.8	6.0	5.3	17.7	19.3	26.5	26.1	
Feb.	2.7	3.9	3.5	4.1	4.0	28.6	48.0	46.1	27.1	22.9
March	2.0	3.1	3.1	4.0	3.7	20.5	28.1	19.9	18.1	15.3
April	.5	1.4	3.0	3.7	2.0	17.7	17.3	14.7	14.5	13.6
May	.6	3.6	3.4	4.1	4.8	15.9	14.5	8.1	10.3	11.8
June	.6	1.7	2.1	2.8	3.5	9.8	10.1	10.0	9.0	11.7
July	.5	.7	1.3	1.8	1.8	4.4	7.0	9.5	8.0	10.5
Aug.	.4	.6	.6	1.7	1.6	3.7	5.3	9.0	8.0	10.4
Sept.	.3	.5	.6	1.6	1.6	1.8	4.4	14.8	15.0	15.5
Oct.	.2	.2	.3	.2	.3	5.6	10.9	12.1	13.6	11.9
Nov.	.3	1.2	2.9	3.5	.3	9.3	11.0	11.0	10.5	10.2

deep into the soil (Purer, '33). The soil in the chaparral area is heavy clayey loam, the size of the grains being exceedingly small, with very little humus content. Distributed through this soil are boulders of varied sizes.

The eight species selected were as follows: *Rhus integrifolia* B. & H., *R. laurina* Nutt., *Nicotiana glauca* Graham, *Photinia arbutifolia* Lindl., *Aplopappus venetus vernonioides* (Nutt.) Hall, *Atriplex semibaccata* R. Br., *Heterotheca grandiflora* Nutt., and *Mesembryanthemum aequilaterale* Haw. The first four mentioned are evergreen shrubs, *Aplopappus* is somewhat woody, the rest are evergreen herbs. *Photinia*, *Aplopappus*, the two species of *Rhus*, and *Heterotheca* are native species, though *Heterotheca* spreads readily in disturbed places and appears to have the status of a native ruderal. *Mesembryanthemum* is native at the coast and probably planted inland, and now an escape. *Nicotiana* is a native of South America, while *Atriplex* is indigenous to Australia. These species were found growing in close proximity at each of the respective stations under approximately the environmental conditions represented by the data collected. During the period of investigation large collections of the leaves were made including the twigs to which they were attached. They were directly placed in tight-fitting tin cans, weighed within an hour after collection and dried at a temperature of 103° C. until a constant weight was obtained. The water content was figured on the dry-weight basis (table II). Leaf measurements were secured from fresh material, mature specimens being used. For both water content and leaf sections representative leaves and stems were obtained, specimens from plants of about the same age and from equal exposures being chosen. Three transverse sections were cut through each leaf, namely, near the tip, the middle and the base half-way between the margin and the midrib. Between two hundred and three hundred leaves of each species having been measured, a

count of at least six hundred sections was obtained of each species at each station. Data for all collections were averaged (table II and fig. 3).

TABLE II. *Differences in leaf thickness and in percentages of water of the eight species in sand dunes and chaparral*

Name of species	Sand dunes Leaf thickness in mm.	Sand dunes Percentage of water	Chaparral Leaf thickness in mm.	Chaparral Percentage of water
Atriplex	.269	244	.204	213
Mesembryanthemum	10.100	912	8.590	873
Photinia	.451	115	.405	114
Rhus laurina	.423	148	.326	139
R. integrifolia	.749	130	.661	91
Nicotiana	.528	677	.536	495
Aplopappus	1.15	980	.443	125
Heterotheca	.221	246	.185	92

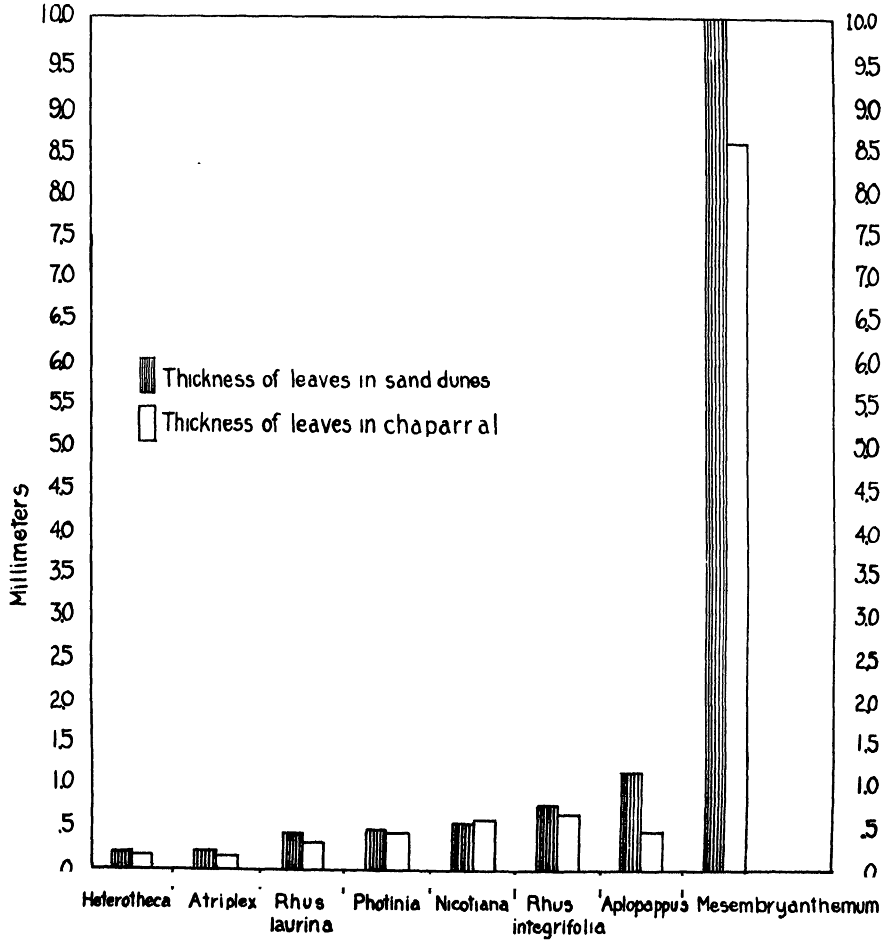

FIG. 3. Differences in leaf thickness of the eight species in sand dunes and chaparral.

Discussion

The periods of precipitation are the same for the two regions, the amount of precipitation being slightly larger in the chaparral area (U. S. Weather Bureau data). The evaporation from the black and the white atmometers is consistently greater at the chaparral than at the sand dunes. Sand dunes are usually known for their high light intensities, but in this case, there is usually greater light intensity at the chaparral area due to the absence of high fog which frequently lies over the coastal area and seldom extends as far inland as the chaparral station. In addition to the high fogs there are low, wet fogs which prevail along the California coast particularly near the seashore and while they at times extend inland they occur but rarely at the chaparral station. At the latter station increase in temperature and wind velocity may increase evaporation.

The maximum soil temperatures at a depth of 30 cm. are higher and the minimum usually lower in the chaparral, giving there a greater range, while in the strand there is less fluctuation. The percentages of soil moisture are higher at equal depths during time of observations in the chaparral area but on account of the difference in the character of the soil it is doubtful if the available moisture is as continuous. The character of the soil differs considerably in the two areas, that of the sand dunes holding water but a short time and being of a very unstable nature; while the soil of the chaparral vegetation may retain the water longer and is of a very compact and stable nature.

As evaporation rates are lower at the Silver Strand and soil temperatures fluctuate less, the conditions for growth, as far as these two factors are concerned, are more favorable there than in the chaparral area. On the other hand, the instability of the substratum, its low moisture content and its small percentage of organic matter render it less favorable for plant growth.

Chrysler ('04) found that plants growing in the maritime situation had thicker leaves than the same species inland and attributed the difference with few exceptions to the greater xeromorphism in the leaves of the maritime specimens compared with those of the inland specimens of the same species. Data gathered, however, indicate that the maritime situation in San Diego is climatically more favorable for plant growth, although edaphically, probably less so.

Conclusions

1. Data on the environmental conditions show that there is less evaporation from the white and the black atmometers and less fluctuation in soil temperature at the sand dune area on the Silver Strand than in the chaparral area fourteen miles inland, while in the latter there is greater soil stability, and higher percentages of soil moisture, in general, prevail.

2. The percentages of water in leaves and twigs are higher in all species at the Silver Strand. The thickness of the leaves is also greater in all species in this location, with the exception of *Nicotiana*.

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REVIEWS

Biology of Termites [1]

As the result of six years of effort, the Termite Investigations Committee with the cooperation of the University of California has brought forth a large comprehensive account of the biology and economic control of termites. This has been a monumental task and the committee deserves great praise for the splendid work it has accomplished. The volume is divided into chapters written by 34 different authors, about half the pages being devoted to the economic aspects of the termite problem.

A number of the chapters are of special interest to ecologists. Kofoid, in his chapter on "Biological Backgrounds of Termite Problems," emphasizes the place of termites in the water and carbon dioxide cycles and the relations of termites, fungi and bacteria to the destruction of cellulose. In his chapter on "Factors Affecting Distribution of Termites," Kofoid discusses the moisture relations within the burrows, the relation of temperature to distribution, and gives an interesting study of the ecological distribution of an oriental termite and its consequent possible invasion of California.

Light, in his chapter on "The Constitution and Development of the Termite Colony," discusses the caste functions and interrelations and gives some interesting data on swarming behavior and mechanisms.

In his chapter on "Some Factors Limiting the Distribution of Termites," Williams summarizes some particularly interesting experiments on the toleration of certain species of termites to carbon dioxide and to moisture and correlates these experiments with the distribution of the species. This work is of such importance in reference to the problems of speciation that it is hoped that a more extensive account of his experiments may soon be published.

The symbiotic, commensal and parasitic relations of intestinal protozoa are discussed by Kirby in his chapter on "Protozoa in Termites." He sums up the evidence for the symbiotic relation of certain xylophagous flagellates to their hosts, and also discusses the evolutionary correlation between the flagellates and the termites. This field is of interest to ecologists because of the beautiful control on the factor of natural selection in the process of evolution. Speciation of the protozoa has often accompanied speciation of the termites. Transfaunation experiments would demonstrate whether natural selection could be considered a factor in the evolution of the protozoa. The evidence so far produced indicates that species of protozoa from rather widely

[1] **Kofoid, C. A., S. F. Light, A. C. Horner, M. Randall, W. B. Herms, E. E. Bowe, and others.** 1934. Termites and Termite Control. 734 pp., 181 figs. *University of California Press, Berkeley.* $5.00.

separated termite species can be transfaunated and will continue to live, thus indicating that the speciation of the protozoa is correlated primarily with the isolation factor. At the same time, speciation among the termites, as indicated by the experiments by Williams, may be the result of natural selection in response to humidity and carbon dioxide together with isolation.

Hendee, in her chapter on "The Association of Termites and Fungi," demonstrates the common occurrence of fungi in the burrows and in the diet of termites and discusses the rôle of termites in distributing fungi.

A division of termites according to their general habitat is contained in Light's chapter on "Habitat and Habit Types of Termites and their Economic Significance." The major categories are damp-wood termites, dry-wood termites, subterranean termites, desert termites, mound-building termites, and carton-nest-building termites.

Many details of the life cycle, habits and distribution of certain species are contained in chapters by Pickens, Snyder, Light, Harvey, Castle, Ehrhorn and Zetek. Details are given for termites of the United States, Hawaii, Mexico, West Indies, Canal Zone, Panama and the Philippines. The details of ecological and geographical distribution and the environmental factors associated with the colonizing behavior are of particular interest in these chapters.

There is still much to be learned about termites and this book should stimulate further research. It would appear to the reviewer that two fields offering opportunity for important results are (1) a more detailed experimental analysis of the behavior mechanisms, and (2) studies of speciation based upon physiological toleration to the associated ecological factors.

The reviewer has found surprizingly few items to criticize in the work, considering its magnitude, and these are not of great significance considering the state of our knowledge at the present time. Kofoid's use of the term "intelligence" (p. 12) is too vague without substantiating experimental data. The suggestions of correlation between dark pigmentation and resistance to desiccation (p. 13), negative phototropism following the swarming flight (p. 18), and the response of the male to odor during the tandem behavior (p. 40) are not in keeping with some experiments of my own on *Reticulitermes* and further data are necessary before these suggestions are validated. In a work which will be of such importance for general reference, it would have been much more valuable to have included a comprehensive index, the lack of which is the greatest fault of the book.

This work will take its place as one of the outstanding contributions to our knowledge of the behavior of social insects, the ecological factors in the life of an important order of insects, and the economic control of an important pest.

ALFRED E. EMERSON

UNIVERSITY OF CHICAGO

Environments in California[1]

The environments and habitats afforded by any given part of a continent depend largely upon three geologic factors:

1. The rocks forming and underlying the surface;
2. The forces which have raised, depressed, tilted and broken them, producing the results known as *geologic structure;*
3. The physiographic changes accompanying and succeeding structural modification. (Physiographic changes of earlier periods are represented by the rocks.)

No American state illustrates these factors more clearly than does California. The contrast between the interior basin, the Coast Ranges, the Sierras and the Colorado Desert are at presen physiographic and climatic; but both are dependent upon accumulation of varied sorts of rock and their deformation in the fairly recent past. In some regions that deformation is continuing today: witness the long series of earthquakes affecting the modern coast.

There also is close relationship between land surface and adjoining marine areas, part of the continental shelf. An understanding of marine conditions represented in Coast Range strata aids materially in a survey of the present littoral belt. Conversely, paleontologists (chiefly engaged in economic work) have solved many of their problems by studying modern organisms and sediments.

For these reasons, Reed's "Geology of California" has special ecologic interest. It surveys, both regionally and historically, the background of present biologic provinces. The historical treatment involves a good deal of what is coming to be known as paleoecology; a compound of sedimentology, paleogeography and natural history of fossils. Past environments, often known in some detail, are described and there are historical summaries closing five chapters which trace the development of the region since Jurassic time. The Jurassic itself remains problematic, despite the extensive work done on it, and illustrates the difficulties of interpretation that sometimes attend geologic research. A summary chapter deals with petrology, structural and historical geology, faunal and floral sequence, and paleogeography.

The adjustment of terrestrial organisms to rising lands is an important problem in both ecology and evolution. California is a case in point, and has been so since the early Mesozoic, with fossils that record both indigenous and invading complexes. Reed's volume reviews these and rescues the state's geologic history from a maze of discrete and apparently conflicting special studies, thus making it of value to biologic as well as geologic users.

Carroll Lane Fenton

West Liberty, Iowa

[1] **Reed, Ralph D.** 1933. Geology of California. Pp. xxiv–355, 60 figs., 27 tables. *American Association of Petroleum Geologists: Tulsa, Oklahoma.* $5.00

ECOLOGICAL LITERATURE RECEIVED

Böcher, Tyge W. 1933. Phytogeographical studies of the Greenland floras based upon investigations of the coast between Scoresby Sound and Angmagssalik. *Meddel. o. Grønland* **104**(3): 1–35. 13 fig.

Böcher, Tyge W. 1933. Studies of the vegetation of the east coast of Greenland between Scoresby Sound and Angmagssalik. *Meddel. o. Grønland* **104**(4): 1–132. 27 fig. 6 pl.

Lemberg, Bertel. 1933. Ueber die Vegetation der Flugsandgebiete an den Kusten Finnlands. *Acta Bot. Fennica* **12**: 1–143. 7 fig. 8 pl.

Stockwell, Wm. P., and Lucretia Breazeale. 1933. Arizona cacti. *Univ. Arizona Bull.* **4**(3): 116 p. 77 fig. 18 pl.

Townsend, M. T., and M. W. Smith. 1933. The white-tailed deer of the Adirondacks. *Roosevelt Wild Life Bull.* **6**(2): 153–325. Figs. 75–169. Pls. 4–5. Map.

Spiker, Chas. J. 1933. Some late winter and early spring observations on the white-tailed deer of the Adirondacks. *Roosevelt Wild Life Bull.* **6**(2): 327–385. Figs. 170–227. Map.

Thompson, D. H. 1933. The migration of Illinois fishes. *Biol. Notes No. 1, Illinois Nat. Hist. Survey.* 25 pp.

Allee, W. C. 1934. Recent studies in mass physiology. *Biol. Reviews* **9**(1): 1–48.

Brown, C. J. D. 1933. A limnological study of certain fresh-water Polyzoa with special reference to their statoblasts. *Trans. Amer. Micr. Soc.* **52**(4): 271–316.

PROCEEDINGS

BUSINESS MEETING OF THE ECOLOGICAL SOCIETY OF AMERICA AT BOSTON, MASS., DECEMBER 29, 1933

The Society met at 10:30 A.M. with President E. B. Powers presiding.

REPORT OF THE COMMITTEE ON THE STUDY OF PLANT AND ANIMAL COMMUNITIES AND THE COMMITTEE ON THE PRESERVATION OF NATURAL CONDITIONS

The study committee devoted most of its energy to perfecting the materials to be embodied in letters to be sent out requesting the adoption of the nature sanctuary plan developed during the preceding year and to the organization of local committees at seven grassland study centers. These local committees are as follows: Texas—Prof. B. C. Tharp, Prof. C. W. Goldsmith, Prof. S. W. Geiser; Arizona—Dr. C. K. Cooperrider, Prof. C. T. Vorhies, Dr. Walter P. Taylor, Prof. William G. McGinnies; Nebraska—Prof. George E. Condra, Prof. J. E. Weaver, Prof. Irving Blake; Oklahoma—Prof. A. O. Weese, Prof. A. T. Ortenburger, Prof. P. B. Sears, Prof. M. M. Shackleford; North Dakota—Prof. H. C. Hanson, Prof. O. A. Stevens; Illinois—Dr. V. E. Shelford, Dr. A. R. Cahn, Dr. T. H. Frison, Dr. A. G. Vestal, Dr. R. S. Smith; Saskatchewan—Dr. K. M. King, Prof. D. S. Rawson, Prof. W. P. Fraser, Mr. H. G. Crawford (Ottawa). They are devoting their attention to developing a plan of research on grasslands to be carried out over a period of about twenty five years. One member of each of these committees is a member of a National Research Council Committee which is seeking support for the researches.

The term of office of this Committee terminates with the Boston meeting. It was moved on the recommendation of the Chairman that the Committee be continued. The Chairman proposed F. E. Clements to succeed the late Dr. H. M. Hall of the Carnegie Institution whose assistance in developing the nature sanctuary program was of especial value. J. R. Dymond was suggested to take the place of Dr. A. Brooker Klugh whose death in a railway train accident was deeply regretted. Dr. Vasco M. Tanner was proposed to take the place of S. B. Locke in the Great Basin and Intermountain area. Mr. Locke takes the place of Professor H. D. Ward as representative of the Isaak Walton League.

The Committee on the Preservation of Natural Conditions sent out letters to the President and various other government officials relative to the placing of the National Park Service. This followed a questionnaire to the members of the advisory board of the study committee. The Canadian members of this board were unanimous (U. S. men very largely) against attaching

national parks to an agricultural service because of its highly utilitarian tendencies, particularly tendencies to modify natural conditions. A series of letters was sent out calling the attention of state representatives on the committee to dangers of too much "clean up" from the Federal CCC activity in state parks and state forests. Too much cleaning up is likely to result in the modification of natural conditions. Members of the Committee have been unusually prompt in answering inquiries and approving or disapproving actions proposed by the Chairman. Dr. Griggs who is located in Washington proved exceedingly valuable in the contacts with government officials.

The chairman requested an assignment of $150.00 from the dues fund of the Society for the work of the Committee during the coming year and requested that to this, the gifts of contributing societies and individuals and the royalties from the Naturalist's Guide be added. The report was unanimously accepted and the reinstatement of the committee granting the funds authorized.

V. E. SHELFORD, *Chairman*

The Committee was commended for its fine work and asked to continue its activity.

RESOLUTION CONCERNING NATIONAL PARKS:

WHEREAS, Many types of reservations, monuments, and buildings have recently been aligned with the National Parks for purely administrative purposes, thus causing confusion in the public mind as to the necessarily superlative character of the natural features hitherto included in the National Park group, as illustrated by the Grand Canyon, Yellowstone National Park, Glacier National Park, Mt. McKinley National Park, etc.;

1. BE IT RESOLVED, That it is the duty of both citizens and governmental officials to understand and to make clear to others that only superlative areas of scenic grandeur, with original vegetation and native animals should be classed as National Parks;

2. BE IT FURTHER RESOLVED, That Congress and the proper government bureaus study the character of the various parks, monuments, reservations, etc., which have been brought together for administrative purposes, and that they classify them as to their appropriate rank and purpose.

Approved December 31, 1933, at Boston by the Society and later by the Committee on the Preservation of Natural Conditions. An additional resolution (No. 2) was approved for sending to the Department of Interior only. The committee was authorized to appoint a sub-committee to classify areas, etc., now under the *Park Service*.

V. E. SHELFORD,
Chairman.

Report of the Official Representative of the Ecological Society of America to the Fifth Pacific Science Congress Held at Victoria-Vancouver, B. C., June 1 to 14, 1933

Although Canadian officials were seriously handicapped by shortness of time due to an unexpectedly sudden decision to hold the Fifth Pacific Science Congress in June, 1933, after an indefinite postponement had been made in 1932, the Congress as a whole was remarkably successful and the section meetings excellent.

Aside from business, social, and official meetings, and a symposium on Applications of Science to Forestry and Agriculture at Victoria, the main activities of the Congress were confined to Vancouver and its vicinity. In Vancouver all program meetings were held in rooms of the Hotel Vancouver where careful attention was given to needs, conveniences, and comforts of the visiting scientists from many parts of the world.

Although Ecology was not represented on many of the programs, general or sectional, by name, there were few programs entirely lacking in papers having some ecological significance. At times, five or six section meetings having papers of direct ecological interest were being held concurrently in widely separated rooms. So far as was observed by the representative of the Society, no meetings of similar rank ever attended showed so much attention to practical problems, and to the possibilities of applications of the different sciences to solutions of these problems. On the other hand, different conversations with members of the Congress showed a lively interest in certain general problems of ecology, *e.g.*, the identification of the "limiting factor" in any particular environment.

As might be expected from the location, the side trips from Vancouver arranged for Congress members were especially interesting to an ecologist, the endless variety in a landscape superficially uniform in general appearance being quite fascinating. The most notable contrasts in detail were brought out by the trip to Grouse Mountain, in which the Congress was taken from the lowlands where vegetation luxuriated in the hot summer sun through levels where snow banks lay higher than the tops of the stages and to the inn at the foot of a slope on which an exhibition of ski jumping was given at 8 P.M. for the benefit of the visitors.

Most, or all, of the papers of ecological interest will soon be accessible in print, but the outdoor illustrations of ecological problems of British Columbia will have to be visited to be fully appreciated.

Respectfully submitted,

Winfred Emory Allen,

Official Representative of the Society

The report was accepted with thanks.

Report of the Committee on Nomenclature

A lengthy report was prepared and mimeographed. Copies were available at the meeting and others have been sent out to some of the members. The first part of the report is printed herewith.

Purposes and Practises

A set of definitions has been assembled by the Committee and is submitted herewith. In accordance with the originally authorized duties (see Ecology **12**: 437–438, 1931), the chief purpose in submitting this list is to aid in clarification and to encourage the more precise usage of terms. When the same term is used in several different meanings the policy of the Committee has been to state various definitions with the idea that people will take their choice or move to bring about uniform usage. The Committee is attempting to point out the usage of the same term in related fields as agronomy, soil science, forestry and meteorology in order to bring about greater uniformity. Where different terms are used for the same concept or where a term has different meanings in various fields the Committee points out such differences and attempts to harmonize them. Occasionally, it has seemed desirable that the Committee recommend to the Society the desirability or undesirability of certain terms, not with the idea of being dogmatic or arbitrary, but to aid in the development of ecological terminology. The Committee hopes that these definitions will stimulate discussion and correspondence. Mimeographed copies of the list have been prepared, not in any sense as a finished product, but rather as a means of getting it into the hands of other people from whom help might be secured. A copy may be had from the chairman.

It might be well at this time to state some basic principles of nomenclature which are guiding the work of the Committee:

1. Natural growth of ecological nomenclature should not be hampered by rules. The Committee can, however, serve as a clearing house and point out what is considered good usage, especially to beginners in the field. Precedent, usage and approval of authoritative bodies are important in the selection of terms.
2. Restricted scientific usage should not violate common literary or general scientific usage.
3. Words long used in a broad sense should not be used in a new, special meaning.
4. Uniformity of usage is desirable in the same field or in closely related fields, as forestry, agronomy, ecology, physiology, soil science, meteorology and geography. If a relatively new word is commonly accepted in one branch of science it should be adopted in other branches when it is needed there.
5. New words should be coined only when there is a distinct need. It is

desirable that ecological literature be intelligible to as wide a field of readers as possible. It is not necessary to have a separate term for every slight difference of meaning.

Words are tools of thought. An exact term may aid in clarifying a clearcut, distinct concept. Ambiguous or inaccurate use of terms may obscure a definite concept. But, the development or formulation of a concept may be hindered by too early coining of new terms or definitions as well as by the failure to use precise terms. Much care must be given to choosing the appropriate terms so that the writer or speaker can convey to others his exact shade of meaning. The Committee believes that the definitions given in the list will contribute toward making ecological terms more efficient tools of thought.

The second part of the report consisting of a " Tentative Glossary of Ecological Terms " defining about seventy-five ecological terms can be secured by writing to the chairman of the Committee.

The chairman requests the continuation of the committee with the substitution of Z. P. Metcalf for R. N. Chapman.

HERBERT C. HANSON, *Chairman*

The report was accepted and the committee continued as requested.

Letters were read from Bradford Williams, secretary of the Massachusetts Landscape Survey showing the kind of work done by the survey in preserving the landscape beauty of Massachusetts. The work was endorsed by the Society and Dr. Shelford was asked to communicate with Mr. Williams.

EDITOR'S REPORT ON ECOLOGY

We have followed the editorial policy reported last year and feel that the results are beneficial.

We have endeavored to keep within the budget suggested by the Business Manager.

The total number of pages published this year is 420 compared to 424 for 1932. In order to keep the number of pages within the limits of the budget, it has been necessary to refuse many papers which would doubtless have been accepted in former years.

ALFRED EMERSON, *Editor*
GEO. D. FULLER, *Assoc. Editor*

This report was accepted in full.

REPORT OF THE BUSINESS MANAGER OF ECOLOGY

For the Fiscal Year, December 1, 1932–November 30, 1933

Receipts

Cash on hand (Statement of 1932)		$1,727.37
Raymond Kienholz, Treasurer, E. S. A.		788.00
Subscriptions, 1933	$1,363.39	
Subscriptions, 1934	436.65	
	———	1,800.04

Single Numbers and Back Volumes		300.18	
Authors' Payments		428.18	
Postage on back numbers		1.08	
Interest, Irving Trust Company		1.65	
			$5,046.50

Disbursements

Printing			
Lancaster Press, Inc.		$3,191.19	
Illustrating			
National Engraving Co.	$433.63		
Jahn & Ollier Engraving Co.	122.99		
		556.62	
Advertising		143.92	
Office Expenses			
Clerical Asst. for 12 mo. @ $10.00	$120.00		
Stationery	34.25		
Postage	74.25		
Wrapping Paper and Cord	2.50		
Telegrams and Postal Expenses—Dr. Emerson	12.12		
Expressage	1.04		
		244.16	
Miscellaneous			
Rock Garden Guide, B. B. G., included in check for subscription	$ .40		
Government tax of checks	.94		
Collections Charge	.49		
Refund for subscription	3.75		
Purchase of back numbers Ecology	5.33		
		10.91	
Balance, November 30, 1933		899.70	
			$5,046.50

Examined and found correct.
December 20, 1933.
H. P. Schoenberner,
Auditor.

Assets and Liabilities

December 1, 1932–November 30, 1933

Assets

Cash in bank		$899.70
Bills Receivable		
Balance due on single number	$ .25	
Subscriptions, 1933	12.00	
Subscriptions, 1934	47.75	
Author's Payment	25.48	
		85.48
		$985.18

Liabilities

None.

Circulation Data as per Mailing List of October, 1933

1. Members	406
2. Subscribers	425
3. Exchanges	97
4. Advertisers	13
5. Editorial Office	2
	943

Number of copies printed per month, 1,275.

C. STUART GAGER,
Business Manager of Ecology

This report was approved and accepted with a vote of thanks.

REPORT OF THE EDITOR OF ECOLOGICAL MONOGRAPHS

On behalf of Mr. Ernest Seeman, Business Manager, I present the following annual report for *Ecological Monographs:*

Publication of Volume 3; 600 pages	$2,988.64
Income from 185 subscribers and other sources	1,702.46
Loss	$1,286.18

The journal lost fifteen subscriptions during the year 1933.

A. S. PEARSE, *Editor*

The report was accepted in full.

The resignation of the Secretary-Treasurer, due to the lack of an academic connection and the consequent lack of time and facilities for properly carrying out the duties of the office was accepted and the following report of the nominating committee presented and approved in full.

REPORT OF NOMINATING COMMITTEE

1. Society Officers:

   President: George D. Fuller,
   Vice-president: Paul S. Welch,
   Secretary-Treasurer: Arthur G. Vestal.

2. Members Editorial Board of ECOLOGY, for a period of 3 years, to succeed Needham, Nichols, Pearson, and Powers: Bertram Wells, F. C. Gates, W. P. Taylor, Francis Harper.
3. Members Editorial Board of *Ecological Monographs*, for a period of 3 years, to succeed Juday and Transeau: Paul B. Sears, A. H. Wright.

The Nominating Committee Recommends:

1. That it be recognized as a policy that the Nominating Committee should be appointed at least two months in advance of the annual meeting, and that it be the duty of the secretary both to call this matter to the attention of the president and to notify him what nominations are called for, including the names of those members of the editorial boards of ECOLOGY and *Ecological Monographs* whose terms expire.

2. That it be recognized as a policy that, except for unusual reasons, members of the above named editorial boards should not be eligible to reappointment until after the lapse of a year following the expiration of their terms of office.

G. E. NICHOLS
E. N. TRANSEAU
A. O. WEESE

The report was accepted in full and the men recommended were elected.

The meeting adjourned at 12:30 P.M.

RAYMOND KIENHOLZ, *Secretary*

NOTES AND COMMENT

Cold Storage Prolongs the Life of Noble Fir Seed and Apparently Increases Germinative Power

The seed of the various species of fir (*Abies*) notably are short lived when held under seasonal air temperature storage conditions and for that reason are difficult to use in any regular reforestation program as seed crops do not occur every year. To determine if the time-honored method of holding tree seed in cold storage to preserve its viability could be applied to noble fir, *Abies nobilis*, Lind., seed, a series of tests was started in 1921 by the U. S. Forest Service at Portland, Oregon.

Samples of noble fir seed held at room temperatures and similar samples held at 15°F. were tested annually for germination over a period of five years. In 1926 the study was repeated, using similar technique. The two series of tests gave strikingly similar results. In both tests all seed showed normal germination the first spring following harvesting, but after the first year no further germination was obtained from the seed held at room temperature, whereas from the seed held in cold storage germination was obtained each year for the entire five year period. In both series of tests maximum germination was obtained from the seed that had been held in cold storage for four years. The per cent of germination obtained in these tests from seed after storage at 15°F. was as follows:

Years in storage	1	2	3	4	5
	P.ct.	*P.ct.*	*P.ct.*	*P.ct.*	*Pct.*
First Series (Started 1921)	14	22	(no test)	34	13
Second series (Started 1926)	21	17.5	16	26.5	18

A cutting test of 300 seeds showed the 1921 seed to be 58 per cent sound and the 1926 seed 38 per cent sound. During the first test a single lot of 300 seeds was used annually but during the second test 600 seeds were used annually for the germination test.

Certain weed seeds are known to improve in germinative power for a period of years; lettuce seed particularly is said to improve up to about the fifth year under proper storage conditions, but the writer has found no record of coniferous tree seed improving in germinative power beyond the first year.

The Boyce Thompson Institute [1] in a two-year test of noble fir seed found very similar germination between seed held at room temperature and at 46°F. after one year of storage; but after two years of storage, seed held at room temperatures showed no germination at all, while that held at 46°F. declined only slightly in germinative power.

Büsgen and Münch [2] say, "With all forest tree seed the germinating capacity falls off with age."

Toumey [3] states that balsam fir, *Abies balsamea*, (L) Mill. is the only species of *Abies* that retains its seed viability until the spring of the second year after harvesting.

[1] **Crocker, Wm.** 1932. In a letter.

[2] **Büsgen, M., and E. Münch.** 1929. Structure and life of forest trees. p. 393.

[3] **Toumey, J. W.** 1916. Seeding and planting in the practice of forestry. p. 104.

He also states that length of storage of all species can be increased by keeping seed in cold storage.

Conclusions

This study very plainly demonstrates that noble fir seed can be held in cold storage for a period of five years without appreciable loss of viability, whereas with storage at room temperatures this seed loses most of its viability after the first year. The highest germination occurred after the fourth year of cold storage; this indicates an unsuspected characteristic of after-ripening for this seed.

To preserve the viability of seed is one thing, but to improve it is something more. If this characteristic is substantiated by further investigation for noble fir or other species, it will be of immense importance to seed collectors and foresters.

Leo A. Isaac

Pacific Northwest Forest Experiment Station, Portland, Oregon

Photosynthesis of Water Plants at Various Depths in the Lakes of Northeastern Wisconsin

During the summer of 1932, studies were made at the Trout Lake Limnological Laboratory regarding the photosynthesis of various water plants at different depths in three lakes of that region. Tests were run on a clear lake with very little color, on a highly colored lake and on a third of intermediate color. Previous determinations of the solar energy at different depths in these lakes had been made by Birge and Juday with the pyrlimnometer.

The method used was essentially the same as that of Marshall and Orr.[1] Glass stoppered bottles containing the plants were suspended at various depths in baskets from a buoy so constructed that its shadow did not interfere with light penetration to the samples. Black bottles containing duplicate samples were run at each depth as a respiratory correction. The amount of photosynthesis was determined by oxygen production as measured by a modified Winkler method. In the early experiments, these data were corroborated by free carbon dioxide and hydrogen ion determinations.

Preliminary experiments were run with weighed samples of Elodea, Ceratophyllum and Chara; only the growing tips were used. In the later experiments, cultures of *Coccomyxa simplex* and *Chlorella pyrenoides* were used. Temperatures were taken at the different depths and the intensity of the solar energy at the surface of the water was read at regular intervals with a solarimeter. Variations in temperature at the different depths apparently had little effect upon respiration.

The optimum depth for photosynthesis was different for the different plants and varied with weather conditions. On a bright day, the optimum depth for photosynthesis during six-hour periods was found at five meters for Ceratophyllum and Elodea in Trout Lake whose water had a color of only six on the platinum-cobalt scale. On dark, cloudy or rainy days, the optimum was obtained at the surface.

The algal cultures gave more uniform results and were more satisfactory as experimental material. The algae were grown in mineral nutrient solutions and were diluted with filtered lake water just before making the runs. In Trout Lake, the maximum photosynthesis of the algae occurred at a depth of one meter on bright days, while on hazy, partially cloudy days, the maximum was found at one-half meter. Exposures of three hours duration proved to be more satisfactory than longer periods; apparently the samples became supersaturated with oxygen in the longer exposures as indicated by bubble formation. The compensation point was found between ten and fifteen meters (fig. 1).

[1] 1928. *Jour. Mar. Biol. Assoc.* **15**: 321–360.

In Mud Lake, with a color of 26 down to ten meters, maximum photosynthesis for the algae was found at a depth of one-half meter on clear days, while in Helmet Lake with a color of 266, it was found at a depth of one-fourth meter. The compensation point was found at six and a half meters in Mud Lake and between one and two meters in Helmet Lake.

A series of three runs was made on Trout Lake, using three hour intervals, in order

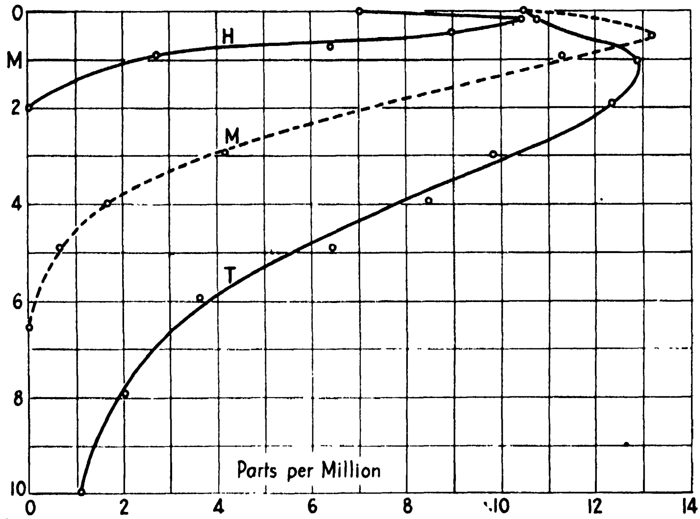

FIG. 1. Oxygen production of *Coccomyxa simplex* at different depths in Helmet (*H*), Mud (*M*) and Trout (*T*) lakes in 1932. The quantity of oxygen is indicated in parts per million and the depths in meters.

to determine the period of maximum photosynthesis during the day for the algae. The first set of the series extended from 7:30 to 10:30 A.M., the second from 10:30 A.M. to 1:30 P.M. and the third from 1:30 to 4:30 P.M. Maximum photosynthesis was found during the second period, that is, between 10:30 and 1:30. In all of the sets, the optimum depth proved to be one meter.

Further experiments were made with the algal cultures in the summer of 1933 in these three lakes and in a fourth, namely Crystal Lake which has the most transparent water found in the northeastern lake district. The solar energy delivered to the surface of the lakes was obtained with a recording solarimeter during each experiment so that the total energy reaching the various depths can be computed from pyrlimnometer readings.

The optimum depth for photosynthesis in Trout, Mud and Helmet lakes were substantially the same in 1933 as in 1932; likewise the compensation points proved to be essentially the same. In Crystal Lake, on the other hand, maximum photosynthesis was obtained at five meters and the compensation point fell a little below 15 meters.

HAROLD A. SCHOMER

UNIVERSITY OF WISCONSIN

WHAT IS AN OPTIMUM?

From time to time, over a period of many years, I have noted in biological literature a strong tendency to use the term "optimum" as though it represented a definite condition, capable of precise identification. I appreciate the grounds for desiring to have such a term, and I approve an honest effort to make accurate statements, but I am not sure that

the use of this term contributes to accuracy within the limits ordinarily assumed. In fact, sometimes I think how nice it would be if I could really identify an optimum, sometime, somewhere. The more I think about it, the less hope I have that I would be able to recognize or describe one if I should find it.

Perhaps the principal cause for harboring this idea lies in the fact that my researches deal primarily with the relation of populations to the complex conditions imposed by Nature. For example, although it is generally understood that Spring is the optimum season of the year for growth of chlorophyll-bearing plants in the Temperate Zone, one is not warranted in assuming that it is merely the *period of time* which constitutes the optimum. Rather, there is reason for thinking that certain biological sequences and certain combinations of natural influences of cyclical trend reach a highly favorable relationship in Spring with a frequency sufficient to give an impression that that season is the optimum of the year. In La Jolla Bay in 1924, marine plankton diatoms were taken in greatest abundance in the Autumn, an occurrence which suggests that the seasonal point of optimum may swing rather widely, even for a general population.

Authentic observations in different parts of the world indicate that in the Summer season a depth of about thirty meters in the sea is optimum for marine plankton diatoms. But there are so many cases in which greatest abundance is found at levels above or below this that it becomes evident that one cannot properly designate an optimum in terms of depth, at least for a general diatom population.

In the sea, as on the land, there are localities which show a tendency to productivity higher than that observed in other places, near or remote. Presumably, some locality is more favorable to abundance than any other, and so entitled to be called an optimum locality, but I do not know of any way of instituting comparisons of favorable localities which will show that one is best (however much *better* it may be). Even if we restrict our comparisons to abundance of the whole populations (of pelagic diatoms for example) this is true, because abundance in all localities must be accurately determined for *exactly the same* periods of time before one can properly conclude that he can identify an optimum locality in that time and for that particular character. At that, one must remember the possibility of error due to the fact that a population may have failed to reach a locality most fitting for it to show abundance, although it may have reached one most fitting for permanence.

It may be suggested, that in a general population the requirements of component species differ to such an extent as to obscure the features which might be used to identify optimum depths, localities and time periods. However, the selection of a given species for examination does not clear the problem of the difficulties already mentioned. Even for land plants under the favoring conditions of the golf course at La Jolla, although it is evident that filaree thrives best in the Winter and Bermuda grass in the Summer, and that both luxuriate on the floor of a certain ravine, it is hazardous to say that in the one feature of growth they have reached the best of which they are capable in those periods, or in that locality. There is good reason to believe that this is true also of plankton diatoms, although less continuous evidence is available. Indeed, it appears that identification of a true optimum in natural or semi-natural relationships requires a fund of detailed knowledge which is beyond human power to reach. Practically, the idea of an optimum seems to have little value in interpretation of natural biological phenomena in spite of its strong appeal to reason.

This impression seems more justifiable as one goes deeper into detailed analysis of the idea of a biological optimum. One of the first difficulties confronted in such analysis is that of isolating or specifying the condition to which the idea is applied. Obviously, one must not content himself with the mere assumption that an optimum is found when the welfare of an organism or of a population is at its best. Welfare is a term entirely too vague and evanescent in application to be useful in this connection. The feature of growth (in the sense of increase in dimensions) has been noted already as one likely

to be selected to indicate optimum influences. However, I do not believe that the greatest increase in volume that is possible necessarily marks the optimum for an organism, or a group of organisms. If that were true, a gardener would not attempt to check a growth of herbage which is getting too rank for his own purposes or for the complete development of his plants. In fact, if one be interested in production of great volume alone, he still does not forget that too rank and rapid growth may reduce vitality and resistance to disease, as well as open the way to other conditions of the organism which may prevent reaching the desired volume.

Furthermore, one cannot go far in the study of living things without noticing some of the differences incident to different phases of a life history. Conditions best for germination of a seed may be far from best for growth (or any other activity) at some other point in the history of any individual plant. Indeed, success in attaining phenomenal growth alone may be due as much to introducing favorable influences at the right point in the life history as it is to any particular refinement in making the combination of influences. How, then, can one ascertain the particular set of factors which combine to constitute the optimum? Similar things may be said about the history of organic activities immediately, or remotely, precedent to introduction of an organism to conditions which are, or should be, optimum.

But, of course, one cannot be content with dealing in such general terms, and he may hope to get a more satisfactory view of the problem by dealing with a single selected influence, as, for example, light. Ignoring for the present the several forms of radiant energy included in what we ordinarily call "light," it seems to be possible for us to treat captive organisms with varying concentrations of light under conditions indicating definite selective responses to the changes in that influence. It is known that a green plant can be killed by a high intensity of light, and that it cannot survive for long under an intensity which is too low. For certain plants, at certain times, and under certain circumstances, it seems to be possible to find a degree of intensity of light which is most favorable, and which it is natural for us to consider to be the optimum.

Superficially, an optimum seems to be so definitely recognizable in some cases, and so nearly duplicated in others, that one is tempted to state that he can find the optimum of light intensity (or of any other influence) for the particular organisms under his observation. I incline to agree with this view until I undertake to apply the tests of the optimum. If it be increase in growth, that may take place at the expense of the longevity, or of the hardihood, or of the reproductive capacity of the organisms. If it be hardihood, then growth may be found deficient. In other words, even by scrutinizing a single feature of organic existence, one cannot be sure that he is viewing at any given moment a combination of conditions which includes a true optimum, although an experienced observer may be able to recognize a serviceable approximation.

Within the limits of my atttention, the term "optimum" is used far more often and more confidently by laboratory workers than it is used by field workers. Presumably, a man who has been successful in keeping a strain of bacteria, or of protozoa, or of mice under cultivation over a period of months or years, is likely to feel that he knows the optima of certain influences very well, *e.g.* optimum temperature. For one thing, he has the very great advantage of being able to try the effects of different conditions on the rejected parts of each generation in his cultures without risking any considerable range in those permitted for his continuous culture. Even so, the question may be raised as to the essential characteristics of the condition which he calls "optimum."

Apparently, the prime essential must be that the influence (say temperature) shall be most promising for the perpetuity of the culture and most favorable to maintenance of what the worker deems to be normal appearance and activity of the culture. In other words, his idea of an optimum is restricted sharply to the demands of his operations, and he is not at all concerned that his culture would perish soon if returned to Nature,

even at the desired temperature. Indeed, it is possible that he may miss the true optimum of his primary concern, the strain tending to run out (or transpose) after ten years at the temperature which he considers optimum, whereas it might run to twenty years without recognizable change from normal if the temperature chosen were slightly different. At any rate, it must be clear that the temperature which he designates as optimum for his purposes is not necessarily optimum for the purposes of some other worker, or for the indefinite survival of the organisms themselves. Since a similar statement must be true of any other influence (" factor ") in the environment, it seems that the term " optimum " lacks much of the precision which usually appears to be intended by its use.

This conclusion becomes almost obligatory when one examines the idea of an optimum in relation to the dynamic (as distinguished from a static or inert) condition of living matter, or of the organisms which it composes. In this connection, even an influence so little complicated as that of pressure becomes difficult to evaluate and impossible to trace. Having applied a certain pressure (atmospheric or some other) at any particular moment in the existence of the organism, how is one to be assured that it is *not* an optimum—or that it *is* an optimum for the conditions of that particular moment? A fundamental characteristic of life is its capacity for continual and continuous change. At any succeeding moment, no organism is precisely what it was in the initial moment of observation. Yet it is from observations in these succeeding moments that one develops an opinion concerning the relation to welfare of a certain pressure at the initial moment. As a matter of fact, the only opinion which he can reach rightly is that the effects of the pressure on a living thing, from the moment of application and through the period of observation, are the best that he has been able to observe; or that they are not so good. They may or may not be highly favorable, no one can really *know* more than that.

Another source of difficulty in finding an optimum is to be found in the problem of tolerances of the organism under observation. So far as I know, tolerances are never adequately tested in connection with attempts at determining optima, and I can recall no case in which their importance has been admitted in connection with any definite records of " optima." Yet it should be obvious that, in Nature, records of " optima " have little value for comparison unless it be known that the tolerances of the organisms compared are similar in range in respect to essential environmental factors. The tolerances of a lichen in a shady nook are widely different from those of its kin in less sheltered spots, and it is true that most experimenters seek to avoid such glaring disparity in character by selecting specimens of similar habit and habitat—so far as can be discerned. But there must be many cases in which the less conspicuous features of tolerance are overlooked or ignored. It is not even probable that apparent limits of tolerances recorded as maxima and minima will give dependable aid in attempts to compare optima. One surely cannot assume that an optimum must be midway between the two extremes. Organisms might have similar ranges in tolerance and still differ in the relative position of the " optima " of various kinds, one being near the maximum, perhaps, while another was near the mean.

As an individual, I doubt that there is an optimum condition of life which is open to human identification. On the other hand, I believe that conditions approaching optima may be observed and described in some cases. In certain instances, I believe that it may be possible to designate somewhat narrow limits within which an optimum may occur. But I do not believe that a true optimum can be grasped, any more than I believe that one can grasp the end of a rainbow. For that reason, I prefer a terminology less rigid than is implied by the word " optimum," *e.g.* " apparent optimum," " the region of the optimum," " bonum," or " super bonum." Surely the usage should be less reckless than it is often seen to be.

W. E. Allen

Scripps Institution,
La Jolla, California

ERRATA

On page 363 of the October 1933 issue (Volume XIV, No. 4) a printer's error occurred in the paper by Gray and Treloar "On the Enumeration of Insect Populations by the Method of Net Collection." The radical should have been continued over the entire quantity for σ_x.

As printed:

$$\sigma_x = \sqrt{\frac{\sum (x - \bar{x})^2}{N}} = \sqrt{\frac{\sum x^2}{N}} - (\bar{x})^2,$$

Should read:

$$\sigma_x = \sqrt{\frac{\sum (x - \bar{x})^2}{N}} = \sqrt{\frac{\sum x^2}{N} - (\bar{x})^2}.$$

ECOLOGY

Vol. XV | July, 1934 | No. 3

THE ECOLOGICAL BASIS OF ANTHROPOLOGY

Griffith Taylor

University of Chicago

The "Zones and Strata" Theory

Perhaps owing to the fact that Anthropology is now treated largely from the cultural point of view, there seems to be a tendency to separate the needs of primitive man too largely from those of the other higher mammals. For instance, certain modern books on the subject state that primitive man migrated in order to seek adventure, to make war, or to gain pearls and gold. Possibly some of these reasons dominated man during early *historic* times, but in the far distant days when man was evolving into the races which are distributed over the world today, the related factors of food, climate and shelter were, in the writer's opinion, all-important, and the other "urges" hardly existed. We may safely assume that the world was relatively empty of man in those distant days of the ice ages. If so, then "pressure of population," "trade incentives," and "laws of trespass" may well have been unknown. On the other hand, it seems likely to the writer that primitive communities might be likely to stay in any environment which they found satisfactory; and that they dreaded the unfamiliar and were loath to leave their homelands, unless they were driven to do so. When migrations occurred, probably the weakest folk moved out first.

Holding these opinions, the writer has for many years felt that primitive man offers exceptional advantages for testing the validity of the "age and area" concept; or, as he prefers to put it, the "Zones and Strata" concept. Speaking biologically, primitive man was a large mammal who left abundant traces of his presence in the form of artifacts, carvings, monuments, place-names, etc., of a type which are not available in aiding our studies of the distribution and evolution of other mammals. The writer was greatly impressed with W. D. Matthew's ('14) classical memoir on the mammals soon after it appeared, and he published (Taylor, '19) a fairly detailed ecological study of the differentiation and migration of man. This was followed by another lengthy study (Taylor, '21) in the same journal and later by a book (Taylor, '27) "Environment and Race." The present paper is an attempt to

describe the mechanism of the migrations, and to incorporate certain significant evidence which has come to hand in the last half dozen years.

The "Zones and Strata" theory as applied to Man starts with the following premises, which are acceptable to most ethnologists.

A. Environment

I. The great land-masses of the world consist of a central continent (Asia) with three "peninsulas," *i.e.*, Europe-Africa, America, Malaya-Australia (fig. 1).

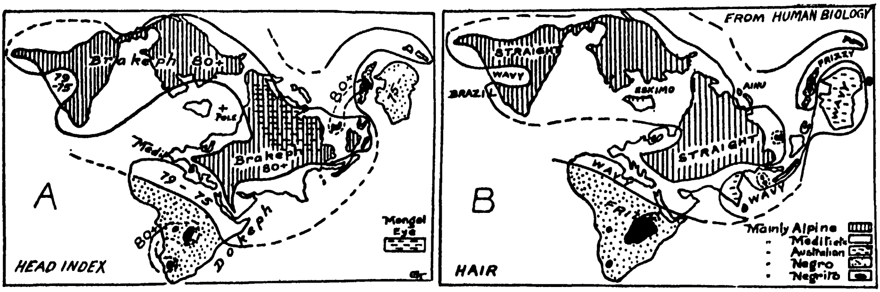

FIG. 1. The Five Racial Zones—as shown by isopleths of head-index and hair texture. Both taken from Biasutti's data (the 75 head-index is added). The three main classes are the Alpine (over 80 and straight hair), Mediterranean (79 75 and wavy hair) and Negro (under 75 and woolly). Australoids have very narrow heads, but wavy hair. Negritoes have woolly hair but rather broad heads (80 +). Note that these classes agree with the zones of migration.

II. Each "peninsula" includes a similar series of nine zones of environment arranged according to latitude (fig. 3 *F*). From equator to pole these zones are: selva (forest), savanna, desert, steppe, Mediterranean evergreen, temperate forest, conifers, tundra, and ice cap.

III. The evolution and migrations of primitive man occurred during the last half million years.

IV. The period was marked in the northern hemisphere (and probably in the southern also) by the great climatic variations known as the Four Great Ice Ages, and by later minor fluctuations.

V. It is easy to show that the vegetation zones (and therefore man's food supply) moved alternately south and north in accord with the waxing and waning of the ice ages (fig. 6).

B. Races in the Old World

VI. The *Negrito* tribes are dwarf, woolly brakephs.[1] They are invariably found in the warmer *marginal* positions of the Old World. They live usually

[1] "*Brakeph*" means brachykephalic (broadheaded) with the breadth of the head *more than 80* per cent of the length of the head.

"*Dokeph*" similarly means dolichokephalic—where the breadth is *less than 80* per cent of the length.

in distant islands, but sometimes in the heart of tropical jungles or in desert areas, *i.e.*, in typical areas of *refuge*. They occur both in the African and Australian "peninsulas" (fig. 3 *A*).

VII. The *Negro* peoples are tall, woolly dokephs.[1] They also are found in the warmer marginal regions but in much larger areas and in larger numbers than the Negritoes. Like the latter, they occur both in the African and Australian "peninsulas." Only a few stragglers of these Negro and Negrito tribes occur in Asia (near Perak) (fig. 3 *B*).

VIII. The *Australoid* tribes are primitive dokephs with wavy hair. They occur in the largest numbers in southern India, which is, of course, a minor "peninsula" from the mainland of Asia. But there are two "wings" of Australoids, of which one extends to the east into Australia with scattered groups in the Malay islands. The western wing is now nearly submerged (fig. 3 *C*).

IX. *The Mediterranean-Nesiot* Race consists of less primitive dokephs with wavy hair. They form a zone extending in an unbroken line from Ireland *via* the coasts of the Mediterranean and Red Sea into northern India. Thence the zone continues through the East Indies in an interrupted fashion and so through Melanesia to New Zealand. It has representatives among the Amerinds and Pacific islanders (fig. 3 *D*).

X. The *Alpine Race* consists of nearly straight-haired brakephs usually of rather stocky build. They form a solid mass of peoples occupying the greater part of Asia and eastern and central Europe. Their salient characteristic is that they dwell in the heart of the Old World—and that there is no essential difference in their racial characters from Eastern France to Corea (fig. 3 *E*). (A discussion of the Alpines in America is omitted in the present paper.)

XI. The evidence in Europe, Africa, southern Asia and Australasia shows an agelong *centrifugal movement* of races from Central Asia (Turkestan or thereabouts). Only occasional and relatively unimportant movements disagree with this general direction of the large migrations in prehistoric times.

XII. Where archeological evidences have been investigated it is found that the *order of super-position* is in general the same as the order of the zones given above. Thus the Negrito stratum is found below the Negroid—or, put in another way, the Negrito migration preceded the Negro, since the living Negrito is always found as an *inlier*[2] surrounded by later tribes. The Australoid is clearly later than the Negro in southern Asia—for millions of Australoids remain in Asia, while practically no Negroids live there. The Mediterranean has "covered" the relics of Australoids in Europe. Finally the outstanding fact in all history is the *Thrust of the Alpine Races*. The Mediterranean peoples have been thrust to the shores of Europe, thrust into Arabia, thrust partly out of India, and almost completely thrust out of China, by the advancing Alpines.

[2] "Inlier" is a geological term for an older formation which projects through a series of younger rocks, which elsewhere cover the older formation.

The writer has used elsewhere an analogous example of zones and strata which parallels the human conditions in almost every particular, and shows how immensely valuable is the ecological point of view in these problems of evolution. He calls it the "*Transport Analogy*." The city of Sydney was for sixty years (1790–1850) the only large town and the center of distribution in Australia. Let us for a moment consider how the methods of transport are distributed around Sydney. During the nineteenth century oxcarts were common in Sydney—now they are found usually more than 200 miles from Sydney. Horse buses became common in Sydney during the latter half of the nineteenth century. These same buses now ply in little towns about 100 miles from Sydney. Motor-buses have thrust these primitive transports to the margin within the last 20 years. Finally aeroplanes are a common sight in Sydney—though still rare in other parts of the large State of New South Wales. The debris from these four types of transport is of course arranged in corresponding "strata" if one examines the junk-piles of the region. In Sydney itself the relics of the oxcart would be lowest—and those of the aeroplane the highest in the heap. The two outstanding features of the distribution are (1) the primitive types function today on the margins, just where they did *not* originate; (2) the greatest number of strata and the latest type of transport occur in the center of the zones, where the stimulus has been greatest.

Almost every feature of the migrations of race is closely paralleled in this analogy, as the following table shows clearly.

The "Transport Analogy"

Zones and Strata	Transport	Race
Center of zones and upper stratum	Aeroplane	Alpine
Second zone and stratum	Motor-Bus	Mediterranean
Third zone and stratum	Horse-Bus	Australoid
Outer zone and lowest stratum	Ox-Cart	Negro and Negrito
Stimulus to evolution	Commercial progress in Sydney	Climatic stimulus in Central Asia

THE CLASSIFICATION OF RACES

Ignoring the earlier attempts at classification, we find that all modern classifications consider skull-shape and hair character. The writer has adopted these as the *chief criteria*[3]—and believes that they are the most satisfactory, for their distribution is in accord with the known movements of primitive people. Such factors as stature and skin color apparently vary much more readily with environment, so that isopleths of these two criteria form a patchwork with little relation to the major movements of primitive man. For instance, the Alpine race in Europe is accepted as a unit which moved slowly

[3] Other criteria are considered also, as is evident from figure 2.

out of Asia from east to west. But it differs greatly in stature in various parts of its habitat. The Mediterranean Race in the same way varies greatly in skin color. The writer thinks it of importance that his own original race maps (drawn up and published in 1919 from available data of head-index and hair) are practically identical with those produced by Biasutti ('12) in his atlas—which the writer did not see till several years later. Biasutti's maps—as being free from any bias towards the "Zones and Strata Theory"—are given in figure 1 *A* and *B*.

The isopleths for head-index (isokephs) are given in figure 1 *A*. There are four major classes, as follows: Alpine, where the breadth of the head is more than 80 per cent of the length; Mediterranean, 79 to 75; Negro and Australoid, 75 to 70; Negrito, usually near 80, is everywhere found isolated in inaccessible places, usually amid dokeph Negroes.[4] The isopleths for hair are given in figure 1 *B*. There are three major classes, as follows: Alpine with straight or nearly straight hair; Mediterranean and Australoids with wavy to curly hair; Negro and Negrito Races with woolly hair. Thus three races are quite distinctive; while the Australoids share with the Negro and Mediterranean, and the Negritoes have woolly hair like the Negroes, but differ from them in most other respects.

The chief available material in anthropology consists of tables of physical measurements and photographs. It is almost impossible to compare such complex data at all satisfactorily, and so the writer was led to devise the

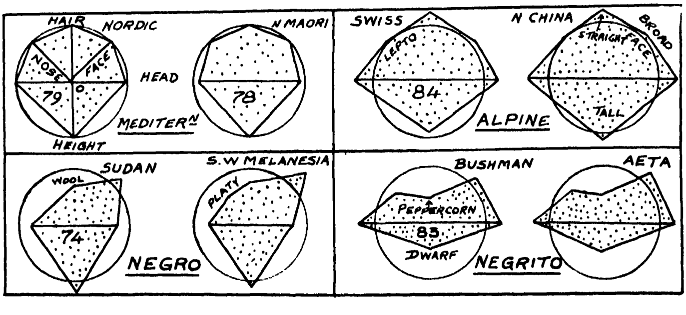

FIG. 2. Ethnographs of four races. Radial distances indicate characters; using Nordic type (in circle) as a criterion. Notice close resemblance (in five major racial characters) of the very distant types (*e.g.*, English and Maori) compared.

ethnograph, which is illustrated in figure 2. It is one of the familiar type of radial graphs—where criteria are arranged in series and given numerical values. I adopted as a standard the best known type of all—the Nordic of Eastern England. The circle in all the ethnographs represents the criteria of the Nordic. Thus *wavy hair* is represented by the upper vertical radius, *leptorhine nose* by the diagonal left radius, *face breadth* by the diagonal right

[4] Note, however, that the most numerous Negritoes, the Aeta of Luzon in the Philippines (and also the newly described Kadar of South India), live far removed from any association with true Negroes. The association does not imply kinship.

radius, *stature* by the lower vertical radius. *Head-index*—being of chief importance in the writer's opinion—is given double value; and the index of the Nordic (79) is accordingly graphed as the horizontal diameter. Shorter radii represent woolly hair, platyrhine noses, narrower faces, shorter stature, or narrower heads. Longer radii represent the opposite criteria. By this means it is easy to compare two individuals or two tribal averages in regard to five of the major criteria. The graphs in figure 2 have been chosen to illustrate the similarities of two distant members of the same racial zone. Thus, the Nordic and Maori (of New Zealand) are seen to be nearly alike, though they are examples at the extreme ends of the same Meditrranean zone. The Swiss and North Chinese are both Alpines. The African and Oceanic Negroes are alike. The Bushman from South Africa resembles the Aeta of the Philippines, and neither has any resemblance to the Negroes.

Present and Past Habitats—The Alpine Race

The series of five maps (*A–E*) given in figure 3 shows the habitats of the five races described above. Their present distribution is shown by the

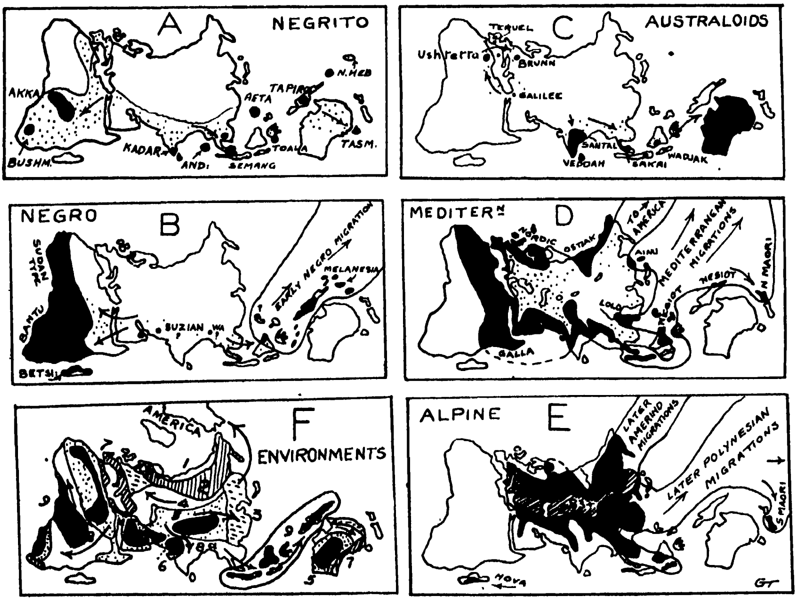

Fig. 3. The five races of Man—present distribution is black. Probable former distribution is dotted. In *E* extra-brakeph tribes (over 83) are ruled. The arrows show main "corridors" of migration. In *F* the major environments of today are shown. 1—Tundra, 2—conifers, 3—broadleaf forest, 4—steppe, 5—scrub, 6 (black)—desert, 7—Mediterranean, 8—savanna, 9—selva (forest). Note Kadar in *A*, and Ushtetta in *C*.

black areas and their former distribution is indicated by dots. It seems to the writer that we have here a remarkable example of the "Age and Area"

concept. Let us consider the latest and best-known distribution first. It is that of the Alpine race, shown at *E*. Here is a solid block of " brakephs " who have unfortunately been divided in some textbooks into two races, Caucasians and Mongolians, for reasons which seem insufficient to the writer. It is true there are obvious facial differences between a slant-eyed Mongolian and a European Swiss. But slant-eyes occur among other races, and are not there made a major criterion. Cheek-bones are more prominent in parts of Scotland than in much of Mongolia. It is impossible to draw a satisfactory line of division between the European Alpines and the Asiatic Mongolians. The people of Turkestan exhibit both kinds of Alpine race—so that to the writer their averages may be taken as the original type from which we have European and Mongolian variants.

It is of interest to see how exactly the belt of the broadest-headed folk (over 83) occupies the center of the zones. Apart from the aberrant Negritoes, there is a universal increase of head breadth as we move from the margin to the center of the zones. If we adhere to the Age and Area hypothesis we are driven to the conclusion that the general evolution of the human race has been in the direction of broader and broader heads. If we accept that the center of the zones contains the latest evolved types, then this belt of Hyper-brakephs (extending from Switzerland to Korea) contains the lasts evolved of the human races. It is hardly necessary to point out that this evolution probably occurred more than twenty thousand years ago—and that the *present* mental, moral and material status of the Turkomans is not of the slightest importance in our discussion. It may, however, be mentioned that there is much evidence that the environment of Turkestan was much more attractive even so lately as B.C. 500 than it is now. It has been, on the whole, drying up ever since that date.

The second feature to note about the Alpine distribution is that it reaches the coast of the Pacific—but does not border any of the other oceans at all notably. This would seem to indicate that the " Alpine Focus " was nearer or more accessible to the Pacific than to the Arctic, Indian or Atlantic coasts. A glance at figure 8 will demonstrate the reason. The great barrier called the " Alpine Storm " (a series of lately-formed high mountains) extends from Spain to China with hardly a break. North of that lie broad plains for the most part—which facilitate east-west movements. Yet farther to the north we have the " Cold-Death Deserts " of the Tundra, which shut off Alpine expansion during most of its race history.

The distribution therefore would lead us to assume a point midway from France to China as the probable center of Alpine expansion. There can be no doubt that somewhere in Turkestan this focus was situated. Early European history deals with influxes of brakephs *via* Anatolia. The Russian steppes have been attacked continuously since the dawn of history by nomads from the Asiatic plains. The history of the Near East is filled with invasions from the north and northeast (only rarely are there large tribal movements

from the south). India has always been invaded from the northwest. Early Chinese history is a record of invasions by the Jade Gate, *i.e.*, from the northwest. All these corridors of migration lead back to one center—near the Caspian and Aral seas. Some years ago the writer pointed out that all recorded history could be summarized in five words, "The Thrusts of the Alpines."

Since the Alpine race is bounded in the east by the ocean we should expect to find some of the earlier Alpines and most of the marginal zone of the next preceding race thrust out to the islands of the Pacific. This is abundantly true, for Alpines are found throughout Polynesia. Moreover, during the last few thousand years there have been long periods when conditions were probably warmer than today in the Old World. Thus in Azilian times and later—say from B.C. 8000 to B.C. 5000—Europe at times was warmer than now. By analogy, northeast Siberia and the Bering Straits may have had a climate much more attractive than it is now. This period probably saw vast hordes of earlier Alpines pouring into Alaska and nearby American lands, as they were thrust onward by the expansions of later Alpines in Asia.

A brief consideration of the "Transport analogy" (p. 226) will show us that these bordering Alpines (thrust into the Pacific and into America) should resemble in general the similarly situated borderland Alpines in Europe. This is indeed the case. The Amerinds and higher Polynesians are everywhere described by laymen as peculiarly "European-looking." In other words, they represent the same early stage of Alpine development as do the European Alpines—and do not exhibit so generally the Mongolian eye-folds, cheek-bones, *etc.*, as do the Alpines of eastern Asia.

It is especially important to note that the Alpines of today are everywhere the *latest comers*. They are the "top stratum," and by the law of "geological superposition" they are the last evolved. Perhaps because much comparative anthropology has been either Nordic or German, this conclusion does not appear to have been published before the writer's memoir in 1919. The past accomplishments of the Alpines have perhaps not quite equalled those of the Nordics during the meager 800 years or so of the record of North European history. But, as regards the future, any student of race should be interested by the fact that Russia controls most of the Alpine habitat of today.

Mediterranean and Earlier Races

Turning now to the ecology of the *Mediterranean* race (fig. 3 *D*) we see that it forms a broken ring all round the Alpine habitat. It is widest and most complete on the south and west—as we should expect. The relics of the Mediterranean zone in the southeast of Asia will be discussed a little later. Something, however, must be said as to the Nordic race.

In several earlier papers and in his book "Environment and Race" the writer has explained why he feels that the Nordics are merely a variant of

the Mediterranean Race (see also Buxton, '25, and Sergi, '01)—modified by their racial history having taken place in cold, moist environments. The Ainu of Japan and other so-called "Paleo-Asiatic" tribes are perhaps to be classed with the Nordics of the Baltic area. The latter are so few in numbers that it seems unnecessary on that count also to erect them into a major race. Their origin is almost certainly in southern Siberia, again close to the common cradleland of man. As with the Alpines so also with the Mediterraneans—we find their lines of migration leading out from central Asia wherever we can check back. It is to be noted that much evidence shows that wide areas of former dokeph tribes (Mediterraneans) have been submerged by Alpines. The Kurgan peoples of Russia and the aborigines of south China are examples. The Nesiot is the East Indian equivalent of the Mediterranean race—somewhat modified by the inevitable jostling with other races in that much broken-up environment. For the same reason the *Pareo-ean* is a variant of the Alpine race in this region.

The racial zone next outside the Mediterranean is the *Australoid* zone (fig. 3 *C*). Here the living representatives are clearly found only in important numbers in the southeast of Asia. There are probably many millions of them in southeast India, such as the Santals, Gonds, and many speakers of Dravidian languages. Representatives are found in the Sakai of Perak, and there are still some 60,000 pure-bloods in northern Australia. Recent research seems to show, however, that this zone originally extended along the Mediterranean Sea and into western Europe. Many skeletons have been discovered—such as those of Brunn (Moravia) which are hardly distinguishable from those of living Australoids in Australia. Fleure and James ('16) describe living people in Wales as approximating to Neandertaloids. The writer wonders if these folk are not also the descendants of the Australoid stratum. Sir Harry Johnston ('23)—the authority on African ethnology—describes the Ushtettas (in the mountains west of Tunis) as "of very Neandertaloid appearance, with much-developed brows, large flat noses, deepset eyes, and in the males much hair about the face and body." He describes them as "similar to the Veddahs, and a little to the black Australians in facial features." Every year skulls are being found which link three interesting races. These are the Australoids, the Negroes, and the Neandertals. Of this type are the Broken Hill skull (Rhodesia), the Galilee skull (Palestine) and the Tamworth skull (Australia). The writer cannot agree with the large number of anthropologists who are satisfied that Neandertal man had no descendants. This type is turning up all over the Old World. It would indeed be curious if he left no descendants, while the Negroes and Australoids were derived from some stock so rare that apparently there are no known fossil examples.

The fourth zone is the Negro race (fig. 3 *B*). Here we have a distribution very like that of the Australoids, save that it is more definitely broken into two widely distant areas. The writer can see no argument in favor of *two*

separate cradle-lands for the African Negroes and for the Melanesian Negroes. Nor does it seem necessary to assume that the Melanesians sailed their canoes from Africa to New Guinea—or that the Sudanese migrated from New Guinea to Africa! The logical conclusion from our ecological studies is that the dispersion from Asia took place so long ago that we cannot expect to find any surviving relics on the mainland of Asia. I have drawn attention in figure 3 *B* to the tribes known as Suzian (Persia) and Wa (Burmah). Both of these have been described as exhibiting some Negro characters—but it is, of course, hard to tell if it was due to an Australoid stratum, a Negro stratum—or conceivably to black slaves. The future will, I think, show that the Negroes also originated in the common cradleland—conceivably far back in the middle ice ages—but the evidence is wanting at present. It is to be noted that the Negroes belong to an earlier (outer) zone than the Australoids. There are plenty of the latter left on the mainland of Asia, where there are no undoubted Negroes. It seems likely to the writer that the Negroes developed in the southwest part of the center of Asia, and so more reached Africa than Melanesia. On the other hand, possibly the Australoids originated in a more eastern portion of the cradleland, hence relatively few proceeded to the west.

The most primitive zone—found in the least accessible parts of the Old World—is occupied by the Negritoes. Their distribution again points to a cradleland midway between their main areas (fig. 3 *A*). The writer cannot agree with the suggestion that they developed from Negroes owing to an unfavorable environment. This might account for the dwarfing—but why it should produce a broad skull, or a convex upper lip or non-Negroid skeleton or paler skins, etc., is not clear to the writer. It is very suggestive that the Negritoes are alike in these respects—whether they live in the heart of a continent, as near the Congo, or in some small volcanic islands, as the Andamans, or in cooler uplands, as in Luzon (Philippines). Nor can the alternative hypothesis that their broad skull links them with the Alpines be accepted. Their whole ecological history is against this theory. We have some slight evidence that Negritoes lived in France at the time of Neandertal man, since the Grimaldi skeletons may be Negrito relics. The writer deduces from their very characteristic habitats today that they were the *earliest* migration of living peoples. He therefore postulates two precursors of modern man; one was Neandertal man, from whom developed the Negro and other races, the other was a smaller, broader-headed type which gave rise to the Negrito (fig. 10).

The Migrations of the Races

The phenomena involved in a racial migration can only adequately be illustrated by a graph which shows the zonal distribution, as well as the evidence of the submerged strata. The block diagram has been used for this purpose by the writer since 1919, and gives a real picture of what has hap-

pened. The conventional "Ethnological Tree" is of little use in this connection, though it illustrates genetic relationships and hence is given in figure 10.

In figure 4 *A*, a simple block diagram of Africa is shown. Here the north is to the right—where Europe is indicated. It seems likely that the Negritoes entered Africa from the northeast, and spread gradually over much of the continent which they found devoid of human occupation—or at best

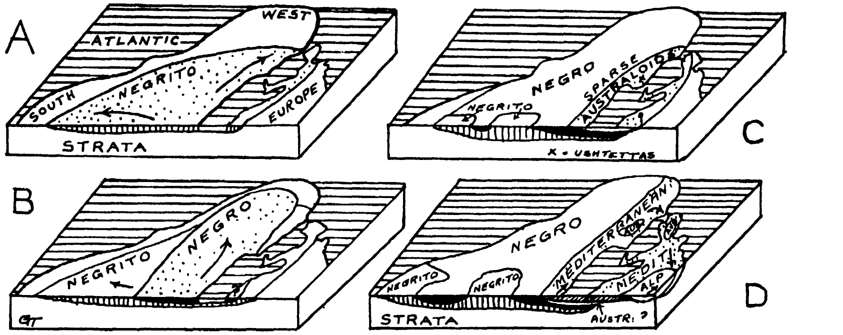

FIG. 4. Block diagrams showing the "zones and strata" theory applied to Africa. Map *A* may possibly go so far back as the Mindel ice age. Map *D* shows the present conditions.

occupied by a few Neandertaloids. We find traces of their carvings in many parts of Africa—notably in Algeria and in Southern Africa. Probably they also lived in France and Spain, where similar pictures occur. It does not seem logical to the writer to imagine that the Bushmen (hybrid Negritoes) carried their art *from Spain* to Cape Colony. This is against the direction of all the major racial migrations. It is, however, possible that Negritoes reached Spain and Cape Colony independently—as the arrows in figure 4 *A* suggest. There are also similar drawings in India—which support the Asiatic origin of the Negritoes. Williamson ('34) describes Negritoes (Kadar) as still living in the mountains in the southern tip of India.

In figure 4 *B* we see the second migration of Negroes, who do not seem to have invaded Europe in any important numbers. Possibly they reached Africa while an ice age was covering Europe, and so naturally kept to warmer lands to the south. But the origin of the Negroes is wrapt in a fog at present. It should, however, be obvious that the finding of an early Negroid skull in Africa merely indicates where the last folk of that sort *died*. Our "Transport analogy" (see page 226) teaches us that primitive skulls are usually found just where the primitive folk did *not* originate.

Following the Negroes came the Australoids (fig. 4 *C*). I show the position of the Ushtetta tribe by a cross. Elsewhere the Australoids have been completely submerged by the Mediterranean Race (fig. 4 *D*). The Australoid stratum is indicated on the front edge of this diagram. The last migra-

tion (overlying all the others) was the Alpine Race—which arrived in Europe in notable numbers about 10,000 years ago. Of course, it was many thousands of years before this that it originated in central Asia. So also we must guard against the idea that the arrival of the Mediterranean Race in Europe corresponded to the period of its origin—which may well have occurred in central Asia some fifty thousand years earlier.

Radial versus Peripheral Migration

The mechanism of the migrations (Taylor, '30) consists therefore in the centrifugal movement of a given race from the Caspian area along several main corridors at the same time. Thus the Mediterranean race (fig. 5) has

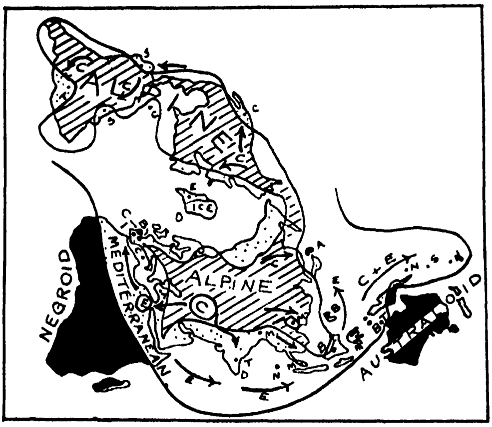

Fig. 5. The habitat of the Mediterranean race shown by dots. Arrows marked *E* show hypothetical diffusion of race and cultures from Egypt—giving a peripheral migration. A radial diffusion of race (and much culture) from the Caspian area (*C*) is more logical. Initials show Couvade sites, from Ling Roth ('93).

come to occupy a semi-circular zone from Britain to Japan (with extensions to the American coasts). It is important to notice that this zone of occupation could have been developed in one of two ways. Some anthropologists have noted a community of cultures along this " Mediterranean Zone "—which, of course, includes Egypt. They conclude that *peripheral movement along the zone* from Egypt (both to west and east) has been the most significant feature of the migration. No doubt some trading has taken place in ships along this route since the dawn of historic times. But the writer believes that many of the culture-facts go back to the common cradleland. The dolmen and menhir culture is associated with this race, but such stones are found far inland in India and the southwest of Asia, where no group of *navigators* was likely to settle. Later investigation will, one expects, show that the inland monuments are earlier than the seaboard specimens, and that both are due to *radial movement* from the Caspian center of dispersion.

Furthermore, it seems unlikely that the extraordinary couvade custom was transferred all around the world by bands of Egyptian navigators (fig. 5). *Couvade* is the custom of the *father* experiencing certain taboos or privileges (such as resting in his hut for a week) after the birth of a child. Ling Roth ('93) has recorded nearly thirty regions where this practice flourished. All that I have been able to identify are confined to the Mediterranean Zone, and are not found either in the central Alpine zone or in the outer Negroid zone. Culture and race in general have little in common, but in this case couvade surely spread *radially* from the common center and was not carried along the "Egyptian Trade Route." For these and other reasons given earlier we may deduce that the semi-circular zone of the Mediterranean race is due to radial centrifugal migrations rather than to *peripheral* journeys along the present zone (fig. 5). Similar reasoning helps to explain the "twin habitats" of the Negroes and Negritoes.

THE CLIMATIC FACTOR IN THE MIGRATIONS

The writer ('21) has published a folding colored plate which illustrates his ideas as to the way in which the ice ages drove out primitive man from central Asia. This aspect of the problem remains nearly as speculative now as then, though it is still the only logical theory in the writer's opinion. However, the Russian geologist Molchanov ('28) has recently stated that northern Siberia was covered with a nearly continuous ice-cap (fig. 9) during part of the Pleistocene. We can, I think, accept it as correct that central Asia experienced more "stimulating" climatic conditions than any other part of the Old World. To the north the conditions soon became too difficult for early man to progress. To the south they became less and less changeable, so that along the equator we had then, as now, a condition approaching stagnation. The region of Turkestan with its changing continental climate, but with much wetter conditions than today so that it consisted of scattered woodlands and prairies, was a very satisfactory region from the point of view of primitive man (fig. 9).

Research in Scandinavia has made it much easier for us to reconstruct the movement of ice-caps, vegetation zones, and of man himself. De Geer and others working on the Varve-clays have dated the moraine of the waning Wurm Ice Age as it developed in south Sweden. They place it about B.C. 18,500. This is shown in figure 6 *A*—where Sweden is shown buried under the great ice cap. Peat bogs in north Germany and Denmark show that tundra plants were growing south of the ice cap at this time. Man had apparently not yet appeared in Sweden.

In block diagram *B* (fig. 6) we see that the ice front has retreated half way along the Swedish peninsula. This is dated about B.C. 9000. At that time the peat bogs in Germany show remains of fir trees, and here also we find the artifacts of Neolithic man. Apparently Paleolithic man found the tundra and steppe very unattractive and so never settled on the Baltic. The

next diagram *C* shows us a further retreat during 5000 years. The fir now covers southern Scandinavia and oak trees cover north Germany. Bronze tools are found in the bogs in the oak stratum—showing that a higher culture has moved north *with the ice retreat.* Finally at the dawn of history, conditions were like those today. The Beech is now the dominant tree on the

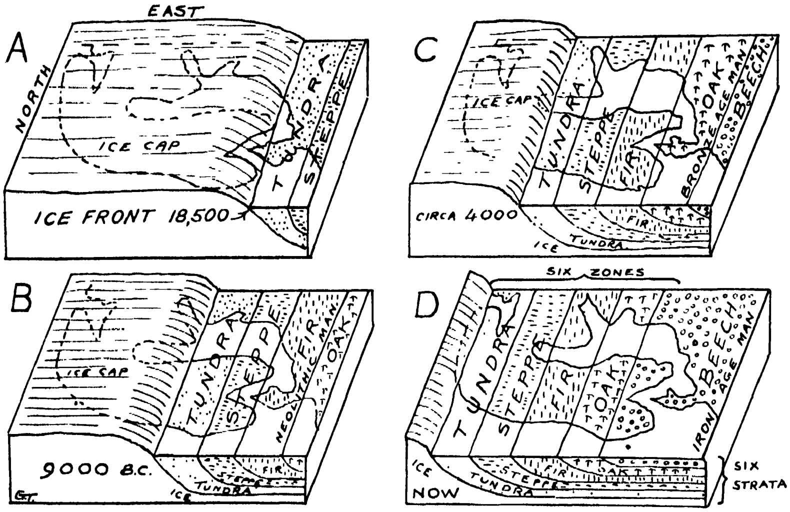

FIG. 6. Block diagrams showing the northward march of the ice cap, the vegetations zones and primitive man in Scandinavia since the close of the Wurm Ice Age. The front of each diagram shows the strata in section. Based on research by DeGeer, Peake, Fleure and others.

Baltic—and its advent was marked by the coming of Iron Age Man. Here, then, we have a *dated* set of zones and strata, and we can be sure that similar movements of vegetation and man, northward and southward, accompanied every one of the ice ages throughout the Pleistocene.

Topographic Changes and Migrations

The topographic changes were less striking perhaps than the climatic during man's major migrations. The East Indies shows the greatest changes known to us. During the ice ages a vast amount of water was locked up in the ice caps around the two poles. It has been calculated that their melting raised the general level of the oceans about 200 feet. Under such circumstance two large areas, Sunda Land and Sahul Land (fig. 7), vanished beneath the waves. Many thousands of square miles, which were no doubt inhabited by many primitive tribes, were submerged. Moreover, the distance between Asia and Australia was increased from 600 miles to 2140 miles. The straits between the "stepping stones" to Australia were also increased in width about three times. Such changes as these certainly occurred during

the last 50,000 years, and must have been of vital importance to the simultaneous migrations of primitive man.

The zoological boundary between the continents is at Weber's Line, shown in the diagram (fig. 7). Here also was the greatest gap which must have

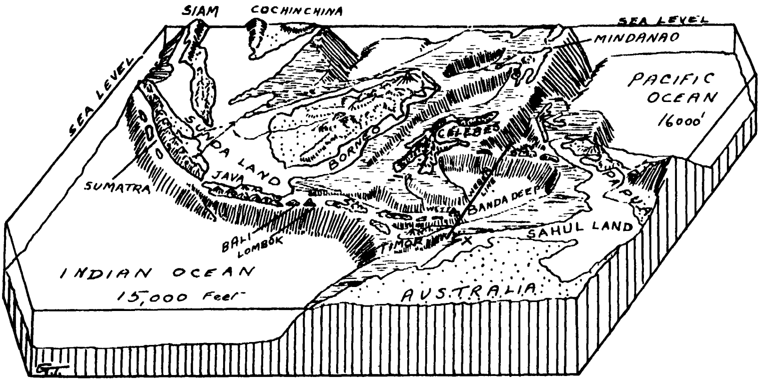

FIG. 7. Block diagram of the sea-floor in the East Indies—showing the "stepping stones" to Australia. During the ice ages the seas were about 75 meters lower—exposing Sunda Land and Sahul Land, so that Timor to X was only 100 miles. The two continents were then only 600 miles apart instead of 2140 miles. "Weber's Line" is the chief biological break. Depths from Molengraaf ('21).

been crossed by the Australoids in their rough canoes. We know that there was no recent *land* connection, since few terrestrial placental mammals ever reached Australia. The recency of the drowning is shown by other evidence. Drowned rivers can be detected on the shallow floor of the Sunda Sea (fig. 7). Freshwater fish of *the same species* are found at the heads of these rivers in Sumatra and west Borneo—pointing to a recent land connection. The chief interest to us, however, is that such remarkable changes would inevitably act to thrust primitive folk *away from Asia,* and prevent their getting back, if they so desired. Thus the drowning of the lands during each interglacial age would act as a sort of "valve" (as I suggest in figure 10), helping to *hold folk at the margins,* who had migrated outwards as the ice cap moved south in the Old World.

Another type of topographic control is illustrated in figure 8. Here is a block diagram of Asia (drawn to scale on the writer's block-drafter) which correlates the Build of Asia with the distribution of the races.[5] The diagram shows the dominant position of the huge 12,000 foot plateau of Tibet. On the west is the narrow Khyber Pass—on the east is the equally narrow "Jade Gate." The latter is bounded on the east by the huge Gobi Desert, and all the migrations into China probably hugged the northern scarp of the Tibetan plateau. Notice also how the complicated fold mountains of Burmah and Yunnan prevent movements from south China to India. In the north are the

[5] Some of the highest peaks have been omitted, as they would hide the background.

open plains of northern Siberia, which, however, were in general too cold to appeal to primitive man.

The laws of migration hold throughout. The weakest are pushed to the wall, the strongest hold the center and the corridors of migration. Thus the latest (broadest-headed) folk are found round the sea of Aral. Surrounding them are allied Alpines who have burst down the Jade Gate and occupied most of China (fig. 8). The aboriginal (Mediterranean) folk have retreated to the rugged hills of Yunnan. The earliest folk (Negritoes) are only found in the Andaman and the Philippine Islands. In the Indian peninsula is an enclosed area—shut in by giant mountains on all sides. Yet Alpines and

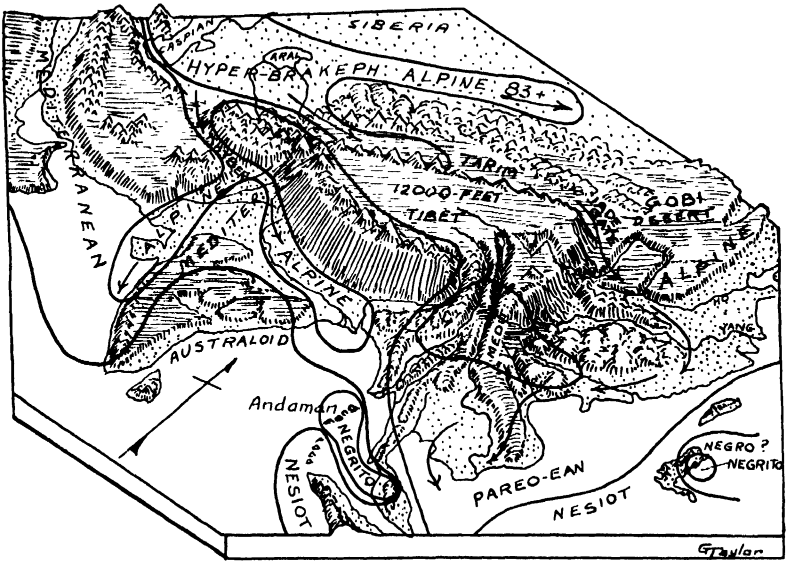

Fig. 8. Block diagram of southern Asia to show how topography controls human migrations. The center of the racial zones is near the Caspian Sea with Alpine types. Pareo-ean (Malay variety of Alpine), Mediterranean, Australoid, Negro and Negrito are successively more marginal. Note the Jade Gate and the Khyber Pass.

Mediterraneans (and Nordics ?) have entered from the northwest. Once they reached India—even if the pressure by the northern populations was released (as the ice age retreated), these Indian settlers would not naturally move back again through the rugged tracks of the Khyber Pass and Afghanistan. For this reason I have labelled such a gateway a "land valve" (fig. 9). It is interesting to note that the Aryan-speakers drove the dark aborigines (mainly Dasyu or Australoids) to the southeast—where they survived in the less attractive hill country of the Deccan. Meanwhile, Alpines occupied Bengal and also conquered the Bombay coast. The Sikhs and Kashmiri nations seem to represent Nordic tribes who settled in the Punjab and thereabouts. The resemblance between this composite Aryan group in India, and

that which invaded Europe is certainly of considerable interest.[6] It suggests that Alpines and Mediterraneans had forgotten racial rivalries before B.C. 2000, when they invaded India.

The Mechanism of the Migrations

In figure 9, I show in a simplified graph some of the main features in the mechanism of the migrations. Let us suppose that the Negritoes and Negroes have left the cradleland in the " region of stimulus " and have migrated along corridors A and B (but mostly to the southwest). One may now postulate a group of generalized folk (like the Galilee or Tamworth type) in

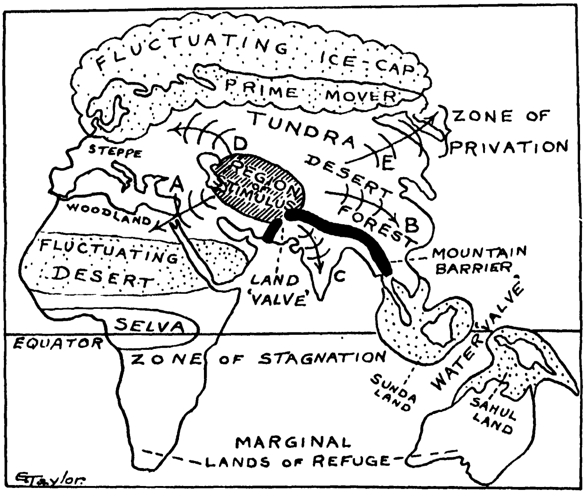

FIG. 9. A generalized map showing the various environmental factors which have determined racial migrations from central Asia. The arrows show where the successive waves moved along the main corridors.

the region of greatest stimulus during the 100,000 years of the next interglacial. (It may have been the Mindel-Riss interglacial, but of this we have little evidence yet.) Under the stimulating and very favorable conditions of the cradleland the Australoid developed. Gradually the Riss ice-cap advanced southwards. The vegetation-zones and characteristic fauna—and necessarily primitive man—moved south also. Apparently most of the Australoids used corridor C (into India), though some used B and others A. Many had left Turkestan far behind by the time that the ice cap began to retreat. As the zones moved northward, just as is shown in figure 6, some of the Australoid type returned to the original cradleland. Those who were in the plains of India were held back by the mountain barrier. There was, of course, no great pressure *on the south* to drive them back, so that they dwelt on unmolested in India for many thousands of years.

[6] These and allied problems of linguistics and race are discussed in the writer's book (Taylor, '27).

During the next great interglacial, also of about 100,000 years, we may suppose that the Australoids in the stimulating cradleland evolved into the Mediterranean-Nordic type. They in turn were driven out by the Wurm Ice Age. Everywhere the Mediterraneans drove the primitive Australoids before them. Thus we find at this period at least two zones in India, two in south-east Asia, and probably two in the Near East. Again the improving conditions moved the vegetation and some migrants back to the cradleland. Alternatively the latter may never have lost all its people. One imagines that some ingenious or stronger folk managed to survive not far from the cradleland (possibly many of the Proto-Nordics survived near the Caspian Sea). They gave rise to the Alpine race, who have not yet moved very far from the center of the Old World except on its eastern coasts. The waves of Alpines, moving down the Indus and Ganges corridors, along the Tarim into China, and round the coast into Indo-China, are shown in figure 8.

With changing climatic conditions the limits of the great deserts and selvas varied very largely. One can readily believe that here also the "corridors of migration" varied in character; sometimes being easier, sometimes blocked by the vagaries of the changing environment. It will be acknowledged that two very definite motives for centrifugal movement from Asia existed: the advance of inclement climate, and of hostile and superior races. On the other hand, there was no similar "drive" back to the cradleland. There were necessarily only weaker earlier tribes on the *marginal* side, if our hypothesis is correct. The climate in the margins would very slowly get hotter and less stimulating, but this would merely slow-up evolution. Indeed, that is why the Negro, who has lived possibly 100,000 years in the tropics (the zone of stagnation in figure 9) has progressed so little beyond Neandertal man as contrasted with Alpine and Nordic types. However stimulating the tropic regions may be to lowly organisms, Man does not experience in the tropics those daily integrations of energy which in the long run produce evolution.

The Genetic Relation of the Races

The last diagram (fig. 10) sums up the biological aspects of the foregoing discussion. The fundamental teaching of racial ecology is that there are twin races in each group, *i.e.*, what we might call a Pacific and an Atlantic twin. For instance, among the Negritoes we find the Aeta and the Congo pygmies—and so all the way up the scale. Hence the ecology demonstrates the likelihood of a common cradleland for each pair of twins. We have corroborated this common cradleland from race-history for the Alpine and Mediterranean groups. It is logical to assume it therefore for earlier groups. Secondly, the breadth-index of the head changes progressively as shown by the numbers in figure 10. Thirdly, the latest developed race is the Late Alpine type—which extends from Switzerland to Korea. Lastly, the most logical conclusion as to the affinities of the Negrito is indicated in the tree.

It is to assume two precursors of modern man living in middle Paleolithic times. This was about 50,000 B.C. in France, but was probably several hundred thousand years earlier in central Asia. These two were Neandertal man and the Proto-Negrito (Grimaldi ?) type. From the former developed the four later races.

If the reader is at all impressed by the value of the " Zones and Strata " (or " Age and Area ") concept as applied to the mammals by Matthew—he will, I hope, be inclined to accept this presentation for the human races as reasonably correct. Matthew shows that the ecology of the tapir, the rhi-

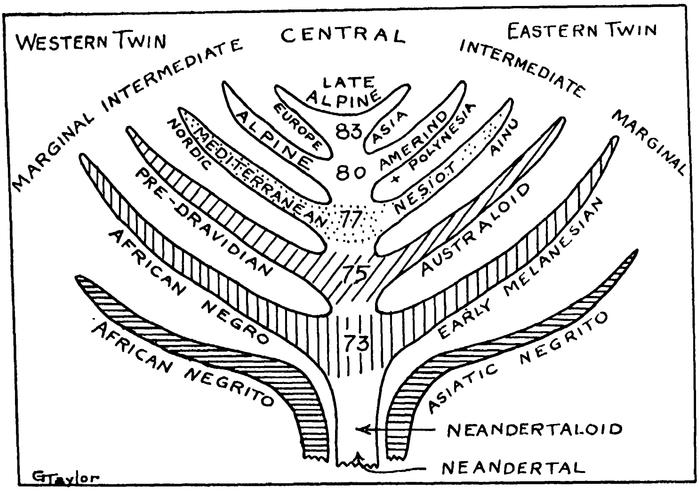

FIG. 10. The racial " tree " showing the relations of the five races. The " twin distribution " is most striking, and indicates a common cradleland for all the races. The Negritoes evolved from a non-Neandertal type, the negroes and the other races from a Neandertaloid.

noceros and the horse, when considered together with their paleontology, is sufficient to demonstrate the order of their evolution and migration. The present writer hopes that he has made out an equally good case for the evolution, migration and relative status of the Alpine, Mediterranean, and Negro Races.

SUMMARY

The paper is an interpretation of the evolution and classification of the races of man by means of the " Zones and Strata " concept. The major races are arranged in five zones about Central Asia, the more primitive types having been pushed to the periphery. Study of the ethnical strata and of the data of the migrations leads the author to believe that the Negritoes, who are now found in the most inaccessible regions, developed first; and were followed in succession by the Negroes, Australoids, Mediterranean and Alpine Races. A number of diagrams illustrate these migrations, and show how the varia-

tion of the climate and environment determined man's movements. The last diagram illustrates the remarkable " Twin Distribution " of races, and indicates that they all originated in a common cradleland near the Caspian Sea.

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THE CLIMAX FOREST COMMUNITY IN ITASCA COUNTY, MINNESOTA, AND ITS BEARING UPON THE SUCCESSIONAL STATUS OF THE PINE COMMUNITY [1]

MARTIN L. GRANT

University of Minnesota

In the literature that has appeared dealing with the vegetation of the northern portion of the Lake States, there appears to be disagreement as to what type constitutes the climax, the special point of controversy being the status of the pine forest, which is the most widespread and characteristic community. In Minnesota the situation is complicated by the fact that the region constitutes a three-fold transition, since conifer forest, deciduous forest and grassland here overlap. Upham, in an early work upon the flora of Minnesota (1884, pl. 1), marked out the approximate boundary between forest and prairie and the approximate southwestern limits of the conifer forest far more accurately than could be done today, after the widespread modification and destruction due to civilization. We can do no better here than to reproduce, in generalized fashion, the boundaries as he determined them (fig. 1).

Itasca County is situated where the two forest types mingle, the grassland not appearing in the picture. The present paper aims to portray the climax community of Itasca County, the fir-basswood association, a mixed association of species, some from the northern conifer forest and others from the deciduous forest. It is believed that the study throws new light upon the problem of the pine forest as climax or subclimax.

Most of the stations studied are located in Itasca County, the others lying to the east in St. Louis County. Itasca County, incidentally, has no connecion except that of name with Lake Itasca in Itasca Park, which lies eighty miles west of the field of this study.

The data herein presented are the outgrowth of field work carried on during the summers of 1927–1929 and 1932, financed and supported by the Minnesota State Forest Service under the direction of G. M. Conzet, Commissioner of Forestry, A. F. Oppel, Deputy Commissioner, and A. E. Pimley, Assistant in Fire Prevention. To these the fullest acknowledgments are due, as it was their assistance, with the cooperation of the late Professor J. Arthur Harris, that made this study possible. Professor W. S. Cooper has served as advisor in the work.

[1] Contribution No. 1 from the Seminar in Plant Ecology of the University of Minnesota.

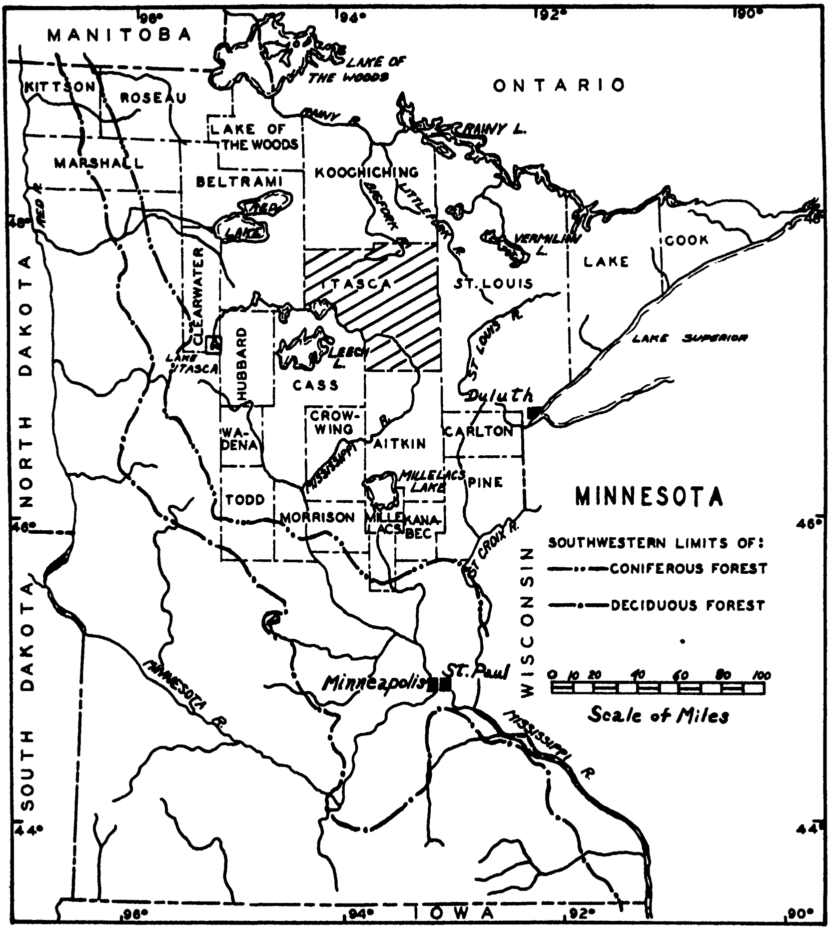

FIG. 1. Map of Minnesota, showing location of Itasca County.

THE GENERAL FEATURES OF ITASCA COUNTY

Physiography

Itasca County covers an area of 2780 square miles located near the center of the coniferous forest portion of Minnesota. Its southern edge is 145 miles north of Minneapolis, and its northern boundary 45 miles south of the Canadian border (fig. 1). The east-west and north-south diameters of the county are each approximately 60 miles (fig. 2). The relief is less than 500 feet, the highest point having an elevation of 1675 feet. Most of the county has a gently rolling topography, with lakes, bogs and swamps in the lowlands and mesic forests on the uplands.

Lakes form the most conspicuous topographic features. While none is of great size, they are scattered in profusion in basins among the moraine

ridges, on outwash plains, and to some extent on the till plains. The northern half of the county drains to Hudson Bay through the Big Fork and Rainy Rivers, while the runoff from the southern half is carried into the Mississippi, which forms the southwestern boundary of the county (fig. 2). In addition to these two main drainage systems, a small portion of the southeastern corner of the county drains into the St. Louis River, which empties into Lake Superior.

There are two principal soil types, inorganic soils resulting directly or in-

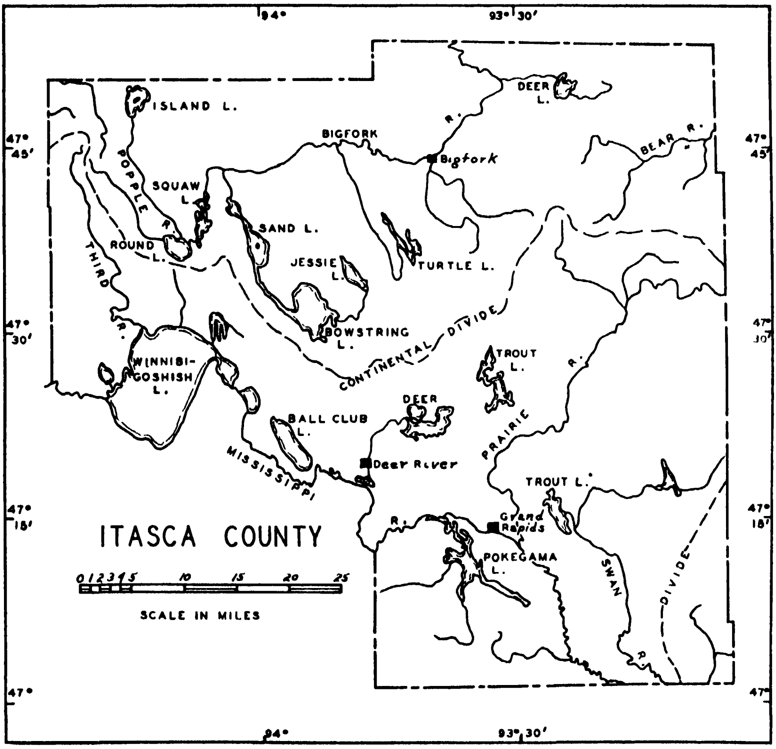

FIG. 2. Map of Itasca County, Minnesota.

directly from glacial deposition, and organic soils or peat. Leverett and Sardeson ('17) divide the surface area of the county as follows:

Moraines (sandy to stony loam)	685	square	miles
Till plains (loam and clay)	775	"	"
Outwash (gravel)	215	"	"
Swamps (peat)	845	"	"
Lakes	225	"	"
Miscellaneous	35	"	"
Total	2780	"	"

The drift varies in thickness up to over a hundred feet; it is usually 20 to 60 feet deep. Rock outcrops are uncommon and local in occurrence. More

peat is found in Minnesota than in any other state in the Union, and Itasca County is one of the four largest peat-land counties. Soper ('19) estimates that there are at least 250,000 acres in the county where the peat is six or more feet thick.

Glaciation

The two early Pleistocene glacial sheets (Nebraskan and Kansan) traversed the whole of Itasca County, leaving a deposit known as the Old Gray Drift, remains of which presumably lie beneath the later drifts. The next glaciation (Illinoian) did not directly affect the county, but during the final one (Wisconsin) there were deposited two layers of drift, known as the Young Red (Middle Wisconsin) and the Young Gray (Late Wisconsin).

The Young Red Drift makes up by far the greatest percentage of the soil of the county. When fresh it is pink or red; it oxidizes to rusty red. It is relatively stony, though without limestone pebbles. The Young Gray Drift is gray, blue-black or buff, and contains light limestone fragments which leach out on exposure, oxidation changing the color of the drift to yellow-brown. It forms a thin mantle over the thicker, more prominent red drift. Except for peat formation there has been but little postglacial deposition. The rivers are shallow, with steep banks, and have not produced floodplains.

Climate

The mean annual temperatures for the three U. S. Weather Bureau Stations in the county (Purssell, '33) are 38.8° F. at both Grand Rapids (18 years record) and Winnibigoshish (46 years record), and 38.0° F. at Pokegama Falls (46 years record). The greatest extremes of temperature recorded have been 103° and — 59° F. (lowest temperature recorded in Minnesota). The mean January temperatures (same stations) are 3.7°, 4.5° and 3.4° F., and the July means 67.7°, 67.9° and 66.5° F. There is a crop-growing season of 100–120 days, though frost may occur at any time of the year. The mean annual rainfall is 22.8, 24.9 and 25.0 inches for the above-mentioned three stations. At Winnibigoshish the average snowfall (14 years record) is 46 inches.

The Climax Forest (Fir-Basswood Community)

Description

The dominant species in the climax forest in Itasca County are the balsam fir, *Abies balsamea* (L.) Mill., the basswood, *Tilia americana* L., the red oak, *Quercus borealis* Michx. and var. *maxima* (Marsh) Ashe, the hard maple, *Acer saccharum* Marsh, the yellow birch, *Betula lutea* Michx., and the white spruce, *Picea glauca* (Moench) Voss. The ironwood, *Ostrya virginiana* (Mill.) Koch, is an abundant subdominant.

The balsam fir grows ordinarily to a height of about 75 feet, and reaches

a diameter of a foot or two. It will endure very dense shade when young, but usually the mature trees require direct sunlight. It thrives best in damp, fairly cool situations, and accordingly may sometimes be found in association with the swamp conifers. The species encounters many natural setbacks. The root system is shallow, and the tree is easily wind-thrown if the forest is at all open. Along with the spruce it is subject to the budworm (*Harmaloga fumiferana* Clemens, and other insect pests. Blister rust, *Melampsorella elatina* (Alb. & Schw.) Arth., and various rots (*Fomes* spp.) are among the diseases which attack it. The larger trees are especially subject to heart rot. In addition fir is not very fire-resistant. Only its tolerance of moisture and shade, and its ability to reproduce prolifically give it the place of prominence in the forest that it holds. The tree seeds at about 25 years of age, usually producing some seed every year. The smaller trees also reproduce by layering (cf. Cooper, '11).

The basswood attains a height of about 65 feet and a diameter of two and a half feet. The trunks frequently grow in clusters, yet in all of the climax areas studied they were solitary. It is slightly overtopped, ten feet or so, by the narrow spire-like tip of the fir, but it has a much broader crown than the latter, and accordingly receives more sunlight.

The red oak is almost as tall as the basswood, and occasionally is equally abundant. It may have a diameter in this region of over two feet.

The hard maple is not a major dominant in the general climax forest, as it does not grow as tall as the basswood, and, judging by its local distribution, does not stand the rigorous climate as well. Along the shores of the larger lakes, however, it is a prominent tree, equalling the basswood in size and dominance. The red oak also reaches a greater size along the shores of large lakes, but it is not so definitely confined to such situations. Rosendahl has suggested that these early-flowering trees, the maple and the oak, are retarded in their spring growth by the cooling effect of the ice and cold water of the lakes until danger of severe frost is past, whereas inland the trees might be frostbitten while still tender and thus be injured. The basswood does not flower until late in July, and thus might not be so definitely affected by early spring climatic reversions. This may account for its more general distribution and dominance throughout the county.

Yellow birch is most commonly found in the swamp subclimax but may persist into the climax. It is not abundant in Itasca County and not so important a forest member as it is farther east in Minnesota.

White spruce, while a conspicuous part of the climax coniferous forest to the north, is here largely confined to the subclimax fir-paper birch association. It apparently cannot endure shade as well as the balsam as it does not survive the establishment of the climax to any great extent, occurring in the latter as a minor element.

Paper birch, *Betula papyrifera* Marsh, is typically absent from the mature

climax, but forests transitional between fir-birch and fir-basswood are much more common than the climax itself.

Below are arranged, in order of importance, the trees found on four quadrats of 100 square meters each near Squaw Lake:

	No. of trees	Average height (feet)	Average diameter (inches)	Amount of reproduction
Balsam fir	9	75	18	160
Basswood	5	65	28	152
Red oak	4	60	25	112
Hard maple	28	40	6	40
Ironwood	8	40	5	280

The following shrubs are characteristic of the mature climax, though shrubs of the subclimax may persist in greater numbers: *Corylus rostrata* Ait., *Cornus alternifolia* L.f., *Salix bebbiana* Sarg., *Prunus nigra* Ait., *Alnus incana* (L.) Moench., *Acer spicatum* Lam., *Crataegus rotundifolia* Borckh., *Amelanchier bartramiana* (Tausch) Roem., *Ribes triste* Pall., *Viburnum trilobum* Marsh, *Dirca palustris* L. and *Rubus pubescens* Raf.

The following pteridophytes are especially abundant: *Pteridium latiusculum* (Desv.) Maxon, *Osmunda claytoniana* L., *Athyrium angustum* (Willd.) Presl., and *Lycopodium annotinum* L.

In its local distribution the fir-basswood climax is largely confined to the loamy soils of the gray drift, being typically absent from the more acid sandy soils of the red drift. Accordingly, since most of the soil surface of the county is either peat or sand, the climax forest is developed only in small scattered areas, and most of the forested region is subclimax. The existence of these three generalized soil types provides a basis for a threefold division of the forests of Itasca County into hydric swamp forests (on peat), xeric upland pine forests (on the sandy red drift), and mesic hardwood or mixed hardwood and conifer forests (on the gray drift). The principal species in the swamps are the black spruce, *Picea mariana* (Mill.) B.S.P., the tamarack, *Larix laricina* (DuRoi) Koch and the cedar, *Thuja occidentalis* L., these in various combinations forming a distinct quasi-stable subclimax. Similarly the pine forests form an edaphic subclimax on the poorer sandy soils of the uplands, the species being the jack pine, *Pinus banksiana* Lamb., the Norway pine, *P. resinosa* Ait., and the white pine, *P. strobus* L. The third division includes the climax trees already discussed and various hardwoods such as aspen, *Populus tremuloides* Michx., and paper birch which are prominent in early stages of succession on the better grades of upland soil.

Relation to Adjoining Climax Types

The geographical extent of this community as a climax is not very great. It is certainly the climatic climax of Itasca County and the adjacent portions of each of the adjoining counties, however, and probably extends over a large area north and south in the central part of the so-called coniferous forest

region of Minnesota (fig. 1). The northern limits of the basswood, hard maple, red oak and ironwood lie about 70 miles north of Itasca County. Further north the balsam and the paper birch, with white spruce, are obviously the dominants, forming the northern conifer climax. At about the same distance to the south the balsam fir loses its dominant role and soon fades out altogether, leaving the basswood and the hard maple as the dominants, with the red oak and the ironwood as important associates. This southern forest is the representative in Minnesota of the eastern deciduous forest, and further southeast the basswood as a climax tree is supplanted by the beech, *Fagus grandifolia* Ehrh., which, with the maple, forms a major association of this formation. To the east of Itasca County, in central Wisconsin, the forest changes to beech and hemlock, *Tsuga canadensis* (L.) Carr., which form still another association of the deciduous forest. To the west of the county, after a series of narrow transition belts, the tall grass prairie begins.

The climax community in north-central Minnesota, then, is a transition forest of fir (and white spruce) from the northern coniferous forest, and of basswood, red oak, hard maple, and yellow birch from the eastern deciduous forest.

The " Pine Climax"

There are many references in ecological literature to the successional status of the white and Norway pines. The most important are here summarized. The region surrounding the northern Great Lakes will first be taken up, then the eastern portions of the range of these species.

Bergman and Stallard ('16), Bergman ('19, '24) and Stallard ('29) advance the view that the Norway and white pines are the climax trees of northern Minnesota. Upham's line of the southwestern limit of the pine forest is reproduced (Bergman and Stallard, '16, fig. 1) as marking the boundary of the pine climax (cf. fig. 1 in the present paper), thus specifically including Itasca and all adjacent counties. Their conclusions are expressed as follows:

" The dominant species of pines of the climax forest are *P. strobus* and *P. resinosa*. The two species often occur in a mixture, or extensive tracts may be occupied by either as a pure dominant. It seems probable that *P. strobus* would finally replace *P. resinosa*, but at present this cannot be confirmed" (Bergman and Stallard, '16, p. 346).

" Cooper ('13) has concluded that on Isle Royale the climax forest is an association of *Abies, Picea* and *Betula,* and he regards this as the climax vegetation of parts of northern Minnesota and north and east into Canada. As concerns Minnesota at least, this does not appear to be the case. The *Abies-Picea-Betula* stage is rather to be regarded as an associes which may in places persist indefinitely as a subclimax. It seems probable that such is the case on Isle Royale. Where these trees are dominant in Minnesota, the islands or parts of the mainland are low, and the water content of the

soil too high permit the invasion and establishment of *Pinus*. With the building up of the soil or as a result of any other change which would decrease the water-content of the soil, *Abies*, *Picea* and *Betula* would undoubtedly be succeeded by the *Pinus* association" (l.c., p. 377).

"The reduction of water content and the ability of pine seedlings to grow in reduced light makes it possible for pines to invade and become established. The actual invasion of the balsam-birch zone must occur in the spaces between more widely separated individuals of that zone. The greater longevity of pines as compared with balsam fir, birch and spruce enables the pines to become dominant in competition with them" (Bergman, '19, p. 68). Similar conclusions are expressed by Bergman in a later paper ('24).

Stallard ('29, p. 543–4) lists four reasons why pines form the mature stage in the coniferous forest: (*a*) "They are perhaps the most shade-tolerant of all the coniferous trees of the state"; (*b*) "The pine trees are higher, attain a greater age and develop stands which cast denser shade than any other trees of the state except dominants of the hardwood climax and dense clusters of spruce and balsam"; (*c*) "The pine relicts, such as stumps, fallen logs and large trees with forms characteristic of those grown in forests, which are now found in small nooks protected from fire, show that denuding agents have destroyed the pines that undoubtedly occupied a large portion of the upland of the state, and this evidence is supported by the accounts of lumbermen"; (*d*) "In the mature stage of the two pine consociations, no other trees are being established. . . . White pine in competition with balsam, white birch and white spruce tends to eliminate them." He also says (l. c., p. 482): "To show that the pines no longer represent the climax dominants, it would be necessary to prove that the climate has changed to their disadvantage, which seems to be contrary to all the evidence available."

Weaver and Clements ('29, p. 440) unite the Minnesota pine forests with the eastern hemlock type: "The lake forest consists of a single association, in which *Pinus strobus, P. resinosa,* and *Tsuga canadensis* are the climax dominants," but they note that the type has suffered considerably from lumbering and fire, and state further that "it is such universal disturbance that is primarily responsible for the doubts as to the actual existence of a pine-hemlock climax, but earlier historical and physical factors have had a large share as well." According to their map (frontispiece) Itasca County is at the extreme edge of this association.

With much of the evidence presented by Bergman and Stallard and by Weaver and Clements there can be no disagreement. White pine is the tallest and longest lived of Minnesota trees. It formerly occurred in much greater abundance than at present. As to its tolerance and ability to withstand competition, however, the evidence does not support Bergman's and Stallard's contentions. Stallard's statement ('29, p. 482) that "pines form the final stage of succession in the coniferous area, except in a few smaller places now

occupied by maple and basswood" is admitted to be partially correct, since from it the inference may be drawn that maple and basswood form stands which are locally climax. The significance of these stands, however, was not appreciated by Bergman and Stallard. The latter explains their occurrence as follows ('29, p. 480): "In many places, where white pine trees are more sparse, are found young basswoods, birches, white elms, ironwoods, or scrub maples, constituting a mictium which has replaced a local area in a damaged climax forest. This mictium is temporary, comparatively speaking, and is hardly general enough throughout the coniferous area to be regarded as a regular subclimax associes."

The view of the present author is that this mictium is a part of the fir-basswood association here presented, which association occurs wherever the soil type permits its development, while the white pine is principally an edaphic climax of the lighter more sandy soils. Similarly, Stallard (l. c., p. 480) mentions "the red pine consociation . . . in whose shade only the seedlings of white and red pine and certain shrubs of the forest floor can persist indefinitely," but studies by the author in Itasca County indicate this to be due to the sandy and acid nature of the soil, the presence of seed trees, and probably root competition, rather than to shade.

Bergman ('24, p. 53) states that in a stand of pine "the absence of trees from the seedling stages up to a diameter of 1.5 decimeters makes it clear that no pines have been able to become established in the forest, at least in the areas represented in the quadrats, during the last 20–30 years. From this it might be inferred that the forest is not self-perpetuating." This fact is obviously contrary to his theory, and accordingly he goes on to show that pines come up in windfalls. It seems apparent that continued catastrophic events are necessary for a pine forest to be perpetuated as such. In these windfalls, according to Bergman, pines are the most numerous species to appear. This, however, may be due largely to the presence of seed trees. He lists fir, paper birch, and white spruce as the important secondary species, but claims they are suppressed by the pine. In this connection Kittredge and Gevorkiantz ('29, p. 51) have shown that in an even-aged stand in northern Minnesota where fir, white pine, Norway pine, and white spruce are coming up under aspen, the pines are the tallest of these conifers when the stand is young, but at the age of 40 or 50 to 60 years, the fir, due to a slightly more rapid rate of growth, has overtopped the others.

Kittredge has stated ('34) that fir, basswood, and hard maple all reproduce under white pine more abundantly than does the pine, and so eventually will replace the pine in any given area. Writing of the white pine forest type in the Lake States in general he says ('25, p. 893) that it is, "if undisturbed, gradually replaced by sugar maple, beech and hemlock, or spruce, balsam and birch." This is certainly true in Itasca County, except, of course, that beech and hemlock do not occur so far west. Kittredge has also declared in con-

versation that the real competition is between the fir-paper birch association and the hard maple-basswood association. It is this competition that has resulted in Itasca County in the development of the transition climax postulated above.

The only other local study in a nearby similar region is that of Lee ('24), in Itasca Park, eighty miles west of Itasca County, in which conclusions very similar to those of the present study are reached. According to this author, the succession on the moister, fertile clay soils leads to a hardwood-white pine edaphic climax, the hardwoods being maple, basswood, elm, red and bur oak, and paper birch, the first of which shares dominance with the pine if the soil is of heavy clay. Lee believed that there was a possible maple climax, as his studies showed that the maple was more shade-tolerant than the pine, and reproduced more prolifically in mixed associations, contrary to the conclusions of Bergman and Stallard. Lee also suggested for Itasca Park a theoretical fir-spruce regional climax, with birch as a third element along lake shores, but this association he found to be now confined to moist depressions. Another of Lee's conclusions was that the hardwood and coniferous forests were separated by a line drawn where the mean annual temperature is 42 degrees and the growing season is of 130 days, on which criteria Itasca County would necessarily be considered as within the coniferous forest region. The fact that Lee was unable to reach definite conclusions as to the true relationships between the maple-pine "edaphic climax," the "possible" maple climax, and the "theoretical" fir-spruce regional climax is an indication that in Itasca Park as well as in Itasca County the true climax is a mixture of fir and hardwoods.

Another study in an adjacent area has given results that throw light on the problem. Cooper ('13) presented the climax on Isle Royale, Michigan, less than 20 miles from the northeast corner of Minnesota, as consisting of fir, paper birch and white spruce. Field studies by various botanists, including the writer, indicate that this association is the climax also in extreme northeastern Minnesota and adjacent Ontario. This region is very close to the northern limits of the hardwoods which are dominant in the fir-basswood transition climax.

The limits of the range of white pine are given by Sargent (1884, map 15) as extending from southern Newfoundland westward through southern Quebec and Ontario to southeastern Manitoba, southeast through Minnesota to east-central Iowa, east around Lake Michigan to central Ohio, around the southern end of the Appalachians to northern Georgia, and up along the east side of the mountains through Virginia and central New Jersey to Long Island. This range corresponds to that of the northern part of the eastern deciduous and the southern part of the northern coniferous forest. That a transition region between these two great forest complexes exists in which dominance may be shared by deciduous and evergreen trees has long been

recognized in many parts of this range, as in Michigan (Whitford, '01; Livingston, '03; Transeau, '05; Harvey, '19; Gleason, '24; Gates, '26), in Maine (Harvey, '03; Moore and Taylor, '27), in Nova Scotia (Nichols, '18), and elsewhere.

Within the eastern and central parts of the white pine range a large number of developmental studies by competent ecologists have been made. It is noteworthy that in none of these treatments is white pine given a climax role. A number of examples follow.

With reference to the region around southern Lake Michigan Cowles early spoke ('01, p. 168) of the white pine as a "xerophytic tree" type which is replaced by oaks and finally transformed into beech-maple forest. Fuller ('11, '14) gives further evidence for the successional role of pine in this region.

In Kent County, Michigan, Livingston noticed the pine stumps but did not reach the conclusion that was later derived by Bergman and Stallard in similar territory in Minnesota. "The ice in its retreat was probably followed northward by vegetation, the pine-heath society leading the way. . . . Then as the soil improved, the oaks became more and more numerous, and the pine seedlings could not develop on account of the shade. The pines thus became fewer in the south and the oaks at last predominant" (Livingston, '03, p. 50). "In some places the pine stumps are so numerous as to raise the question whether the hardwood is not an entirely recent development. It is probable, however, that scattered maples and beeches were mixed with the pine, and that on the removal of the latter their seedlings simply took possession of the ground and shut out the pine seedlings" (l. c., p. 52). Further north, in Roscommon and Crawford Counties, pine is shown to grow on poorer soils (Livingston, '05, p. 37): "Of the upland series, the hardwood type of vegetation seems to need the most water, the most soluble content, and the most humus. . . . The types of white, Norway, and jack pines seem to require less water in the order of their arrangement."

Harper, writing of northern Lower Michigan ('18, p. 27), came to similar conclusions: "On the more clayey soils the original forests evidently were mainly of hardwoods and hemlock, making a dense shade and considerable humus. On the most sterile sands forests of jack pine prevail, while in intermediate habitats, covering most of the upland area, white and red pines seem to have been the dominant trees before the lumberman apppeared on the scene."

In extreme northern Michigan Whitford was first to show ('01, p. 300) that white pine was not the climax type: "As a rule, the white pine seems to occupy the tension zone between the coniferous and the deciduous forests. If the climate be unfavorable for a higher type of forest tree, however, a stage beyond the white pine forest is not reached. If the forest be not too open, and if surface fires are absent, the deep shade established by the pines

means that the edaphic and atmospheric factors have become favorable for establishing the climax forest of the region. . . . The broad-leaved deciduous trees produce a still deeper shade, so that if any pine seedlings are able to survive in the pine forest, the increasing shade will finally make it impossible for a new generation of pine trees. The development of beech and maple seedlings, however, is not affected by the shade of the parent trees." Harvey ('19, p. 216) gives a similar treatment for Lake County: "Upon this basis the southern peninsula should then be considered as a northern extension of the deciduous climax forest formation" and further: "It is apparent, therefore, that the yellow [Norway]-white pine complex is the expression of a combination of edaphic factors which exclude the climax type" (Harvey, '22, p. 29). Gleason ('24) and Gates ('26) showed the hardwood forest to be the climax in Cheboygan County, with pines strictly successional: "The poorer or sandy uplands were covered with pine forest (*P. strobus* and *P. resinosa*) grading rather sharply into beech-maple forest on the better soils of the uplands" (Gates, '26, p. 171).

In northwestern Pennsylvania Lutz was not certain whether hemlock-beech or hemlock alone was climax, but white pine is given as a minor element in the climax stands: "The poor distribution in size classes is attributed to the inherent inability of white pine to reproduce and maintain itself under a dense virgin forest canopy, especially such as exists in a hemlock-beech forest" (Lutz, '30, p. 16–17).

Similarly for the Adirondack region and New England (Cooper, '22, p. 8): "White pine . . . finds its principal home within the area controlled by the northern phase of the deciduous forest, and plays a successional role leading toward the ultimate establishment of that type." Also in virgin forests in Connecticut (Nichols, '13, p. 213–214): "The third remnant . . . differs from any of the preceding in that the dominant tree is *Pinus strobus*. Hawkes describes the trees in this group as 'the most magnificent white pines that can be found in the East, fully equal to the best timber in the Lake States.' Many of them tower up to a height of 45 meters and have diameters of nearly a meter. It is a significant fact, however, that although the pine includes most of the mature trees here, the rising generation is composed mainly of hemlock, with a sprinkling of sugar maple, yellow birch, beech, and other hardwoods. Obviously pine does not represent the ultimate type." Lutz ('28) in general follows Nichols' treatment, listing the white pine as of "seldom" occurrence in the hardwood forests of southern New England.

On Mt. Desert Island, Maine, Moore and Taylor ('27, pp. 113–114) do not consider the white pine as a climax tree: "The white pine type occurs in the successional series on the lighter well-drained soils. Only on abandoned clearings does it occasionally take possession of heavier soils. On the lighter soils white pine reproduces well in the openings and will form an important component of the next higher stage in the series, the mixed conifer. Its com-

petitors, the spruce, fir, and cedar, able to endure more shade, increase in proportion at the expense of the white pine, but never eliminate it because there are always openings which give it a chance." Nichols ('18, p. 294) reports that "white pine is a frequent constituent of the climatic climax forest throughout the transition region; but when growing in pure stands, it probably represents either a temporary association or else an edaphic climax." On Cape Breton Island, N.S., "It is particularly characteristic of the steep, well-drained rocky slopes and ridges which flank many of the larger streams" (Nichols, l. c.).

In a general paper on the forest types of the eastern United States, The Society of American Foresters' Committee on Forest Types ('32, p. 12) speaks of white pine as "a long lived temporary type seldom succeeding itself except after fires or under special cultural treatment."

It appears from the preceding discussion that with regard to the general range of white and Norway pines a very large majority of workers consider those species as forming a community of *subclimax* status. The only exceptions are Bergman and Stallard who claim for them climax rank in northern Minnesota (the statements of Weaver and Clements are based upon the work of these authors). Even here their contention is disputed in two published investigations, by Lee and the present writer, and in unpublished field studies by a number of workers. It would seem that the evidence to date is overwhelmingly in favor of the successional status of the white and Norway pines. Bearing in mind that a community may differ in status under differing climatic conditions, it is evident that further studies of an intensive sort are desirable, in which both ecological and physiological methods should be used.

Summary

The climax plant community of Itasca County, Minnesota, is the balsam fir-basswood association. Other important trees in the climax forest are red oak, hard maple, yellow birch and white spruce.

This climax forest is of a transitional nature, two of the dominants (fir and spruce) being drawn from the northern coniferous forest to the north and northeast, and the rest from the eastern deciduous forest to the south and southeast. This transition is probably the climax community over most of the coniferous forest region of Minnesota, except the extreme northeastern corner of the state.

The climax forest is largely restricted to the heavy clay soils of the gray drift, and thus is local in its development. On the sandy red drift there is present a conspicuous edaphic climax of Norway and white or jack pines, and on peat soils is found an apparently stable subclimax swamp forest of black spruce and tamarack or white cedar. Since most of the surface of the county is red drift or peat, these two types, the pine forest and the swamp forest, cover an area many times greater than does the climax.

The evidence from the literature and from unpublished observations is overwhelmingly in favor of subclimax status for the white-Norway pine community over its entire range.

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STUDIES IN MASS PHYSIOLOGY: THE ACTIVITY OF GOLDFISHES UNDER DIFFERENT CONDITIONS OF AGGREGATION

FRANK SCHUETT

Whitman Laboratory, University of Chicago [1]

Activity in animals has been recognized for some time as an important element in the determination of many physiological problems. While an estimate of activity has been made several times in several different ways, no successful laboratory attempt has yet been reported in dealing with fish movements under unencumbered conditions. Devices such as the ichthyometer (Spencer, '29) are ingenius efforts to obtain the total activity of fishes, but except for the large fishes this apparatus introduces serious errors because the fish is placed under circumstances so remote from natural conditions that its behavior is far from normal. For the determination of endurance under anaesthesia this type of apparatus should suffice to give accurate estimates, but for normal, unhampered movements the fish must be free. Another method of investigation is the determination of oxygen consumption and the subsequent correlation of this with activity. This method, although theoretically valid, runs into technical difficulties which make interpretations difficult. The writer (Schuett, '33) reported cases of differential oxygen consumption in grouped and isolated fishes of various species. In the determination of oxygen consumption of aquatic forms, however, it has been generally overlooked that the production of nitrites may lead to an error in the analysis of oxygen by the Winkler method. In spite of reports (Orr, '26) that nitrites are not a product of animal metabolism, nitrites have been found in nitrite-free water in which fishes and fresh-water mussels had lived under standard laboratory conditions for from two to twelve hours, in quantities sufficient to affect the proper determination of oxygen by the Winkler method. For a general discussion of the applicability of the Winkler method in respiratory work, see Allee and Oesting (in press).

In order to test the effect of nitrites upon the analysis of oxygen, one type of the writer's former experiments was repeated, using the Rideal-Stewart modification of the Winkler method, which corrects for the nitrite error. The results of ten such experiments are shown in table I.

[1] The writer is indebted to Dr. W. C. Allee for the use of Whitman Laboratory during the course of this work, and for suggestive criticism.

TABLE I. *Showing the difference in oxygen consumption between grouped and isolated goldfishes. Results recorded in cc. per fish per liter*

Oxygen consumed	
Group of four	Isolated
0.46	0.58
.40	.53
.37	.27
.45	.45
.44	.57
.34	.36
.39	.35
.40	.37
.44	.40
.41	.45
Mean = 0.41	0.43

Instead of finding a statistical significance far above the threshold as previously reported for the unmodified Winkler method (Schuett, '33), the index of significance, according to Student's method, is found to be 0.4444, a figure which indicates a complete lack of significance.[2] The mean and standard error of these experiments compared with the identical statistics of similar experiments using the unmodified Winkler method are as follows:

	Group of four	Isolated
Unmodified Winkler method	0.362 ± 0.029	0.642 ± 0.032
Rideal-Stewart modification	0.410 ± 0.011	0.433 ± 0.030

Instead of a decrease in the oxygen consumption of some 44 per cent, as was found in the unmodified Winkler method, a figure of undeniable significance, the Rideal-Stewart method shows a decrease of only 5 per cent.

The oxygen consumption method, too, largely involves the use of containers or respiratory chambers whose size is distinctly too small, as results of the present paper will bring out. Furthermore, oxygen consumption is not a very direct method for the measurement of activity, and many things can affect the consumption of oxygen other than activity.

The method used here for the determination of activity is the most direct possible. For this method the writer is indebted to Mr. Raúl Escobar. All sides of an aquarium were marked off into squares, and observers were stationed at right angles to each other with eyes at the aquarium level. From these two angles the movement in any direction, on the part of the fishes, could be ascertained. The squares on the walls of the aquarium were drawn so that each side was 5 cm. in length. This divided the volume of the entire aquarium into imaginary cubes 125 cc. in capacity. In passing from one cube to another there are only three alternatives, the distances of which from any one cube are 5.0, 7.1, and 8.4 cm. The distance has been calculated on the basis of center to center of the cubes. The fish did not always reach the center of a cube, but some standard is necessary to avoid subjective reactions on the

[2] In Student's method a figure of 0.01 or less is regarded as having statistical significance.

part of the observers. This reaction has been cut to a minimum, since a fish is usually either on one side of a pencil line or on the other, the base of the dorsal fin being used as the index structure. By means of previously arranged signals the notes could be compiled into a composite, and the exact distance travelled by the fish accurately determined.

The size of the squares is of considerable importance, since a variety of movement is possible within a single square if the dimensions are sufficiently large. On the other hand if the size of the squares is too small there may be difficulty in deciding which square the fish is actually in, especially if the movements are relatively rapid. In the work to be reported goldfishes of 3.5–4.0 cm. were used.

The Movement of Goldfishes

Individual fishes show a great variation in their activity. Even within a single species there may be found relatively sluggish individuals and comparatively active individuals. This, however, need not introduce a source of error, since it is possible to follow a single fish through a wide range of conditions. With the background of individual fishes in view, their response, in the way of activity to varying conditions of crowding, can be readily measured. In the following study goldfishes (*Carassius auratus* L.) have been used exclusively. This species has been a standard laboratory animal for many years and is not known to show a typical schooling or shoaling reaction.

The purpose of this study has been to determine (1) what influence, if any, was exerted on any particular fish by the presence of others in the same group, and (2) what effect the size of the aquarium had on the individual fishes. Aquaria of two sizes were selected, similar in shape, but one double the capacity of the other. The volumes of the aquaria were respectively 7.5 and 15 liters.

The fishes were examined in daylight from north windows in every case. After being placed in aquaria, the fishes were allowed to stand for twenty-four hours before being tested, and were never observed except under quiet laboratory conditions. After records were taken the fishes were fed and changed to other conditions and allowed to stand for twenty-four hours. The water was changed each day, an artificial pond water being used exclusively. This water was made by adding salts to distilled water in the following quantities: 58 mg. $NaNO_3 + MgSO_4 + K_2SO_4$ in equal amounts and 116 mg. $CaCl_2$ per liter.

Records were taken with a stop watch over a representative period of activity and results calculated to centimeters travelled per hour. The fishes were used in groups of 1, 4, 8, and 16 fishes. Only fishes of distinctive color patterns were selected for examination, as these could be easily followed, even in the larger groups. The activity of only one fish was followed at any given time. The results with eight such fishes are summarized in figure 1. In these experiments the same fishes were tested in different sized groups, and

their activity recorded. The behavior in the different sized groups is well brought out by this graph. Individual records do not vary appreciably from this summary.

A number of interesting points are evident from this graph. It appears that there is a definite optimum size of group for each size of aquarium, judging the optimum size by the minimum activity. This size is near four in the 7.5-liter aquaria, and approximately eight in the 15-liter tanks. Such results

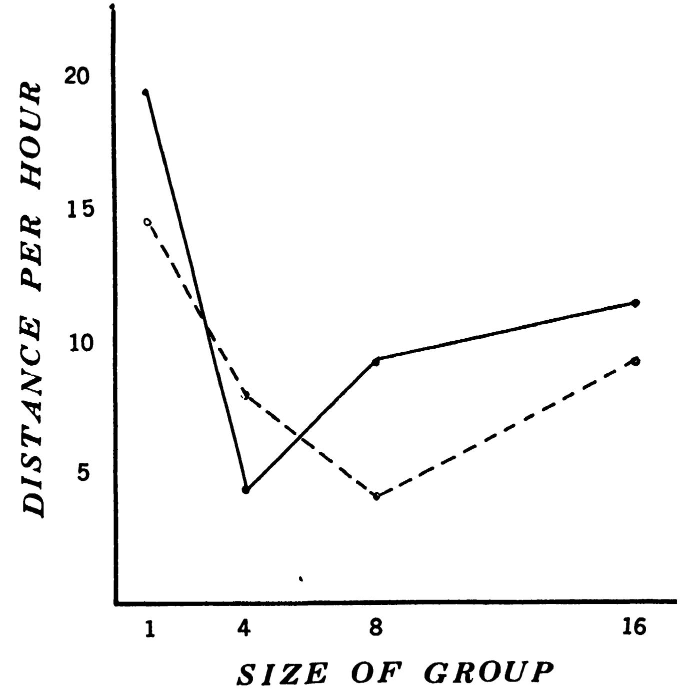

FIG. 1. The difference in activity of goldfishes according to size of group and size of aquarium. Distance measured in thousands of cm. per hour. Solid line for 7.5 liter aquaria; dotted line for 15 liter aquaria.

appear to be consistent. Above the optimum number activity seems to increase, probably because of added stimulation of some kind from the larger groups. This stimulation, at least in the smaller aquaria, is greatest in the interval between four and eight fishes, and there is additional evidence that the same is true of the larger aquaria in the interval between eight and sixteen fishes. The nature of this stimulation is not as yet clear, but evidence indicates that the movements of one fish visually observed have a pronounced effect upon the movements of others. Thus, the analysis resolves itself into an intragroup problem. Whatever the nature of the stimulation, however, it is clear that in groups larger than the optimum there is a noticeable increase in activity.

The effect described above was not seen in connection with work on the oxygen consumption (Schuett, '33). This may be because of the fact that the respiratory chambers used in oxygen consumption work are of such a size as to produce a crowding effect upon the contained fishes, causing movements that would otherwise not occur. In such experiments the fishes were seldom quiet in the respiratory chambers, usually moving in vertical paths from bottom to top in the chambers. This was true both with isolated fishes and with groups of four. Under these circumstances the effect of quieting, as usually noticed in the groups, was lost, as the results here indicate.

An attempt has been made to ascertain whether the type of water, or amount of previous conditioning by allowing other fishes to live in the water first, had any effect upon the activity shown. Both well water and the artificial pond water were used, but no essential difference in the behavior of the fishes, as evidenced by their activity, was found.

Group reactions are not unknown in goldfishes. Welty ('34) has shown that the reactions of goldfishes are conditioned, partly at least, by the presence of others in the aquaria. The present report adds strength to this conclusion. Work is now in progress to analyze the nature of this group reaction.

Summary

1. The amount of movement of goldfishes is shown to be a function both of the number of individuals present within a given group and of the size of the container.

2. A criticism of previous methods, and of results obtained by the Winkler method (unmodified) of oxygen consumption is given.

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THE RELATION BETWEEN FREQUENCY INDEX AND ABUNDANCE AS APPLIED TO PLANT POPULATIONS IN A SEMIARID REGION

W. G. McGinnies

University of Arizona, Tucson, Arizona

The problem of determining the relative or absolute abundance of the component plants of both small and large communities is of great importance for adequate analysis of ecological relationships. Chart and list quadrats of various sizes, transects, and other means of sampling have provided considerable information for small areas, but do not entirely serve the needs where the stand or community under study has a wider range. As it is obviously impracticable to count the number of individuals of each species within a large community, many workers have turned their attention to some rapid method of sampling. Probably the most common system used is the " frequency index "[1] method of Raunkiaer ('09, '18). This investigator marked off a number of plots (usually 25) one-tenth of a square meter in area. The species present on each area were noted but the individuals were not counted. The percentage of plots on which a species occurred was designated as its frequency per cent.

Since this pioneer work by Raunkiaer, many investigators have tested the method under a wide range of vegetative conditions throughout the world. The methods used and the results obtained by Raunkiaer were made more available to English-speaking workers through translations by Smith ('13) and by Fuller and Bakke ('18). The investigators who have used and discussed this method include: Arrhenius ('21, '22, and '23), Gleason ('18, '20, '22, '25, and '29), Kenoyer ('27), Hanson and Ball ('28), Hanson and Love ('30), and Romell ('30). The general consensus of opinion seems to be that it furnishes a good basis for the comparison of plant communities, although there has been some discussion as to its degree of accuracy and its possible variations.

The present study was undertaken with the purpose of testing the method under semi-arid conditions, and, if it proved basically sound, to use it for comparison of changes occurring within certain plant communities, and for a means of comparison between plant communities of different habitats. The present paper is devoted to a consideration of the literature and a presenta-

[1] " Frequency index " is used here as the equivalent of " frequency " and " frequency per cent " of some of the earlier papers dealing with this subject. The term " frequency index " is used, as the values obtained by this method are indices of frequency rather than exact frequency values.

tion of the experimental results pertaining to the relation of frequency index to abundance. The size and number of quadrats which would yield the most reliable information were given some consideration, but the principal aim has been to determine as nearly as possible the exact relationship between frequency index and abundance if any such definite relationship should exist.

Number of Quadrats Necessary for Significant Results

Within a given stand of vegetation of a normal degree of homogeneity, each additional quadrat should decrease the average deviation. Beyond a certain point, however, additional quadrats will not reduce the deviation sufficiently to justify the labor expended. The determination of this number depends in part on the heterogeneity of the stand of vegetation, and in part on the standards of accuracy set by the investigator.

Raunkiaer thought that 25 to 50 quadrats located in a straight line gave the optimum results when time and accuracy were both considered. Gleason ('20) recommends that the homogeneity of the community should be taken into consideration in making a decision as to the number of quadrats to be used. If possible, 100 should be tallied. The number would be dependent in part on the size of quadrat used. Large quadrats would include a greater number of species and hence fewer quadrats would be needed to furnish adequate frequency index figures for the less abundant species. Kenoyer ('27) concluded that 25 quadrats gave essentially the same results as a larger number. Hanson and Ball ('28) used 50 quadrats to represent each condition in their studies of the influence of grazing on the composition of vegetation. Later, the same investigators used 30 quadrats of various sizes in a similar study. In all the work cited above, the number of quadrats used was more or less arbitrarily chosen to fit the conditions under observation.

In the present study, the number of plots to be used was calculated on the basis of chance distribution. In the majority of cases the quadrats were evenly distributed over an area of 10,000 sq. m., so that the number of quadrats of various sizes to give the required accuracy could be computed. As a recorded frequency index cannot be less than 1, the lowest possible frequency index (expressed in per cent) for 25 quadrats would be 4, and for 50 quadrats would be 2. This tends to accentuate the deviations, but in addition to this, it was found that under the experimental conditions there was a decrease in the deviation between comparable frequency indices with an increase in the number of quadrats used.

In all determinations, at least 100 quadrats were recorded and in the majority of cases 200 quadrats in two series of 100 each were tallied. An increase in accuracy was obtained up to 200, but above 100, it is doubtful if the increase sufficiently compensated the time expended.

The Relation between Frequency Index and Abundance under Ideal Conditions

There has been considerable discussion as to the relation of frequency index to abundance. Some have assumed that the frequency index is directly proportional to abundance, while others, notably Gleason ('20), Arrhenius ('21), and Romell ('30), believe that it is not. They indicate, however, that the relation between frequency index and abundance can be more or less accurately expressed by curves or equations.

In order to test the mathematical relations between frequency index and abundance and to determine the amount of variation under ideal conditions, a simple laboratory test was made. It was planned that the laboratory test should possess the same proportions as the work in the field, that is, a square centimeter would be equal to a square meter in the field. For these tests, a table was constructed with a cloth-covered square top one square meter in area, with a ridge or shoulder completely surrounding the top. Beads of different colors, each color representing a different abundance, were evenly sprinkled over the top to secure a reasonable random distribution of each color. A 10 sq. cm. square frame with a 1 sq. cm. compartment inserted in one corner was constructed. This double frame was used to mark off simultaneously areas of 10 and 1 sq. cm. for frequency index determinations. The table top was marked with easily visible guide dots in two series of 100 each. The *A* series was evenly spaced in 10 rows of 10 each and the *B* series located at equally distant points on the diagonals of the *A* series. After the beads had been distributed, the double frame was set down squarely with a dot in its center and each different colored bead present within each frame was checked on an appropriate form. The records for the 10 sq. cm. frame and the 1 sq. cm. frame were kept separately. No record was kept of the *number* of beads within the frames but merely whether or not one or more beads of given color were present. This was repeated successively for each guide dot in the *A* series, then in the *B* series. The beads were then collected and redistributed and the sampling repeated. The purpose of running two sample series each time the beads were distributed was to check the regularity of distribution. As the records for each quadrat were kept separately, irregularities could be checked. The calculations used here were based on 10 repetitions each of the *A* and *B* sample series. The results obtained are shown in table I.

Table I shows that there is a distinct difference between the total number of beads which might be expected to lie within the areas represented by a sample series and the corresponding frequency index. For example, the area of the table top is 10,000 sq. cm. and the total area represented in a series of 100 10 sq. cm. samples is 1000 sq. cm. With perfect random distribution, there should be 1000 brown, 500 orange, 250 lavender, 120 black, 100 red, 80 gold, 50 yellow, 30 green, 20 pink, and 10 blue beads within this area. On this basis the brown, orange, lavender, black, and red might be expected to

TABLE I. *Frequency index for a given number of beads distributed at random, on an area of 10,000 sq. cm.*

Color of beads	Number of beads	Mean frequency index for 10 sq. cm. quadrats	Mean frequency index for 1 sq. cm. quadrats
Brown	10,000	100 ± 0.024	64 ± 0.401
Orange	5,000	99 ± 0.083	42 ± 0.443
Lavender	2,500	90 ± 0.401	22 ± 0.388
Black	1,200	69 ± 0.521	12 ± 0.302
Red	1,000	62 ± 0.362	10 ± 0.350
Gold	800	55 ± 0.531	8 ± 0.252
Yellow	500	40 ± 0.432	5 ± 0.229
Green	300	26 ± 0.350	4 ± 0.202
Pink	200	17 ± 0.262	2 ± 0.147
Blue	100	10 ± 0.271	1 ± 0.092

give a frequency index of 100, but the experimental results show a frequency index approaching 100 only for the brown and orange beads. The frequency index decreases successively to 62 for the red which represents a very significant difference from 100.

The explanation of this difference may be found in the sampling method. If the average number of beads on the entire area is 1 on every 10 sq. cm. it would not mean that every area selected of 10 sq. cm. would have a bead on it. Even if the beads were perfectly spaced at 10 cm. intervals, it would be possible to turn a 10 sq. cm. frame so that it would not have any beads within it. If the total number of beads were counted on 100 quadrats, it would be found that some of the individual quadrats would show 2 or more beads while others would not have any. The total would closely approach 100. However, the frequency index method only measures the " hits " and " misses," and under the conditions outlined above there will be many " misses."

At the lower end of the scale there seems to be a closer correspondence between the total number of beads in 1000 sq. cm. and the frequency index. Random distribution would allow 10 blue, 20 pink, 30 green, 50 yellow, and 80 gold beads for the combined area of a sample series. The difference between these numbers and the mean frequency index varies from 0 for the blue to 25 for the gold beads in regularly increasing magnitude. The explanation for the closer approach of frequency index to the average abundance in lower frequency ranges is, that as the total number of individuals becomes less the average distance between beads is greater and hence the likelihood of more than 1 bead occurring on any given 10 sq. cm. area decreases. Thus the frequency index tends to give the same results as counting where the individuals are widely spaced.

The frequency indices for the 1 sq. cm. sample series show substantially the same thing in a smaller magnitude. The total number of beads on the 100 1 sq. cm. samples would approximate 100 brown, 50 orange, 25 lavender, 12 black, 10 red, 8 gold, 5 yellow, 3 green, 2 pink, and 1 blue. The frequency index is identical with the abundance (with one exception) up to an abundance of 12, beyond that, there is an increasing divergence between abundance and frequency index.

To determine the relation of frequency index (FI) to abundance, curves were plotted with abundance on the x-axis and the frequency index on the y-axis. It was found that the curves thus secured approximated the curve derived from the equation $FI = 1 - (1 - 1/q)^n$ suggested by Gleason ('20). This equation according to Gleason was used to determine the FI for n plants on q quadrats. Applying this to the bead data, the equation may be expressed as $FI = 1 - (1 - 1/100)^n$ or $FI = 1 - 0.99^n$ [2] where $n =$ Total beads/10,000 multiplied by the area represented in a sample series of 100 quadrats. Thus for computing FI for the lavender beads, n would equal $(2500/10{,}000) \cdot 1000 = 250$ for the 10 sq. cm. sample series and $(2500/10{,}000) \cdot 100 = 25$ for the 1 sq. cm. series. The essential difference in the equation as compared to its use by Gleason is in the calculation of n. Gleason counted the number of plants on 100 quadrats, while in the above case it is calculated on the average number per square centimeter. The relation of frequency index to total abundance as expressed by the equation is identical for both frames. The resulting curve is shown in figure 1. Total

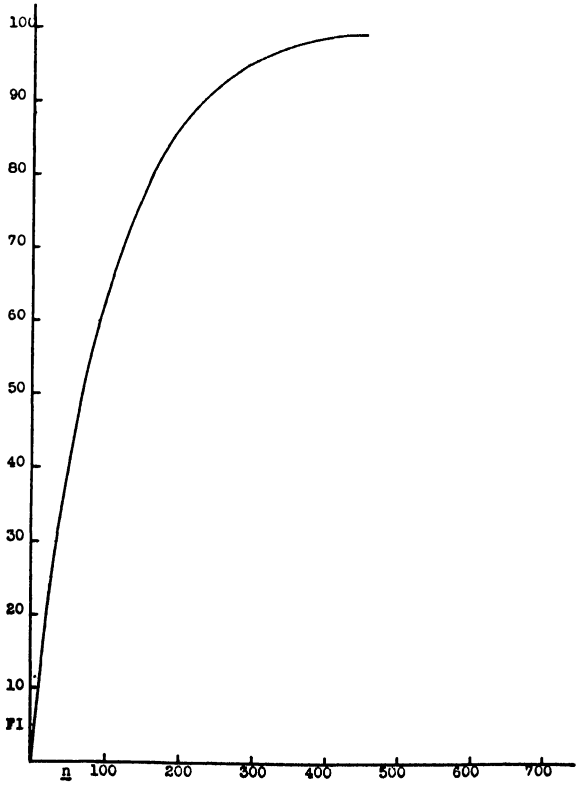

FIG. 1. Relation of frequency index to abundance. For total abundance, multiply by 10 for the 10 sq. cm. quadrats and by 100 for the 1 sq. cm. quadrats.

[2] The resulting quantities are usually expressed as whole numbers.

abundance for the entire area can be determined for the two sample series from the experimental frequency indices by multiplying the corresponding *n* by 10 for the 10 sq. cm. series and by 100 for the 1 sq. cm. series. The degree of fit to the calculated curve was determined by computation of the residuals, standard error, alienation and correlation indices, as suggested by Bruce and Reineke ('31). The essential data for these calculations are given in table II.

TABLE II. *Comparison of experimental frequency index for beads with values obtained from curve*

	10 sq. cm. quadrats					1 sq. cm. quadrats			
n	Exp. FI	Curve FI	Diff.	Diff. sq'd	*n*	Exp. FI	Curve FI	Diff.	Diff. sq'd
10	10	10	0	0	1	1	1	0	0
20	17	18	−1	1	2	2	2	0	0
30	26	26	0	0	3	4	3	+1	1
50	40	40	0	0	5	5	5	0	0
80	55	55	0	0	8	8	8	0	0
100	62	63	−1	1	10	10	10	0	0
120	69	70	−1	1	12	12	11	+1	1
250	90	92	−2	4	25	22	22	0	0
500	99	99	0	0	50	42	40	+2	4
1000	100	100	0	0	100	64	64	0	0
Total	568	573	−5	7		170	166	+4	6
Avg.	56.8	57.3	−0.5	0.7		17.0	16.6	+0.4	0.6
Standard error			0.84		Standard error			0.77	
Alienation index			0.027		Alienation index			0.039	
Correlation index			0.99		Correlation index			0.99	

The figures in the columns marked "difference" represent the departure of the experimental frequency indices from those calculated from the curve. The average difference in both quadrat series is less than 1 bead, minus in the 10 sq. cm. quadrat series and plus in the 1 sq. cm. quadrat series. Although the sum of the differences should be zero with a perfectly fitted curve, the deviations are well within the possibilities of experimental error, so that the equational curve was adopted as the standard.

Having thus established the relation between frequency index and abundance under conditions of rather ideal random distribution, and having determined that the equation suggested by Gleason was fundamentally sound, experiments were then conducted in the field to determine whether or not these basic relationships existed under the average distribution of species and individuals in the various plant communities.

In preliminary field tests, quadrats with areas of 0.1, 0.25, 0.5, 1, 2, and 10 sq. m. were tried in numbers ranging from 25 to 200. The large quadrats, however, did not give an adequate range in frequency indices for the determination of the relative abundance of the more common species. It was found that the 1 and 2 sq. m. quadrats gave the best range of frequency

indices for the greatest number of species, but that the species with the greatest abundance were differentiated much better, as to relative abundance, by the smaller quadrats. On the basis of these results, it was decided to use quadrats of 1 sq. m. and 0.1 sq. m. for the field determinations of the relation between frequency and abundance. A suitable square meter frame was constructed of ½ in. pipe with a 0.1 sq. m. frame set in one corner, so that the 1 sq. m. quadrats included the 0.1 sq. m. quadrats. Each series of 100 quadrats was laid out at regular intervals within a square area 100 m. on a side. The 1 sq. m. quadrat series would then represent a 1 per cent sample and the 0.1 sq. m. series would represent a 0.1 per cent sample. On the basis of the bead results, 100 1 sq. m. quadrats, evenly distributed over an area of 10,000 sq. m., should include all species with an abundance of 100 or more, and to furnish more or less significant frequency indices for species with an abundance up to 50,000; and 100 0.1 sq. m. quadrats should give significant frequency indices for species ranging in abundance from 1,000 to 500,000. The entire range of frequency indices would thus include all plants with an average abundance of 1 plant on 100 sq. m. to 50 plants on 1 sq. m.

The field method was based on that used with the bead tests, that is, square plots 100 m. on a side were laid off, then starting 5 m. south and 5 m. east of the northwest corner, 100 quadrats were located in 10 north and south rows of 10 each. This was designated as sample series *A* and, in most cases, a sample series *B* was run east and west, starting from 10 m. north and 10 m. east of the southwest corner. In this way the two sample series were entirely independent, but so arranged that they should be strictly comparable. The usual method was to locate each line of quadrats by means of stakes or flags and to locate the quadrats by pacing. Each time that a quadrat was located, the frame was set squarely in front of the operator, just touching his toes and with the 0.1 sq. m. inset frame always on the right hand corner nearest the operator. Records were kept on a special form on which a block of 100 numbered squares was used for each species, and if the species were present on a given quadrat, an *x* was placed in the square on the form corresponding to the number of the quadrat. By this means, irregularity in the distribution of any species could be checked. Plants rooted within the area marked off by the frames were marked with an *x* on the form, and overhanging plants were designated with a small circle. Only the *x*'s are used in the basic calculations. Frequency index data were collected on 41 different plots located in various parts of Arizona. On 27 plots, both sample series *A* and *B* were run; on the other 14 plots, only one sample series was run. Frequency index determinations were repeated twice for 6 series and three times for 12 series, in different years, making a total of 98 determinations of 100 for both the 1 sq. m. and 0.1 sq. m. quadrats. On some of the sample plots, counts were made of the number of individual plants of some of the representative species. In each case, all the individuals of a given species were counted on both the 1 sq. m. and 0.1 sq. m. quadrats for the entire series of 100 quadrats. Alto-

gether, 298 plants on the 1 sq. m. and 277 on the 0.1 sq. m. were counted. The species to be counted were selected on the basis of ease of counting and representation of the entire range of frequencies. Not more than 10 species were selected on any one plot.

The vegetation in which the plots were located varied from desert grassland to yellow pine forest and might be divided into three general zones: Desert Grassland, Intermediate, and Yellow Pine Forest.

The Desert Grassland in Arizona lies mostly between elevations of 2000 to 4000 ft., with a rainfall of 12 to 18 in. Characteristic plants include: Rothrox grama, *Bouteloua rothrockii*, black grama, *B. eriopoda*, mesquite, *Prosopis velutina*, and several species of *Aristida*.

The Intermediate zone includes short grassland, chaparral, sagebrush, and pinon-juniper woodland, lying between elevations of 4000 to 6800 ft., with annual precipitation of 15 to 22 in. The short grassland is characterized by blue grama, *Bouteloua gracilis*; the chaparral by oaks, *Quercus turbinella*, and others, and mountain mahogany, *Cercocarpus* spp.; the sagebrush communities by the mountain sagebrush, *Artemisia tridentata*; and the pinon-juniper woodland by pinon pine, *Pinus edulis*, and junipers, *Juniperus utahensis* and *J. monosperma*.

The Yellow Pine Forest, characterized by western yellow pine, *Pinus ponderosa*, lies between elevations of 6800 to 8000 ft., with an annual precipitation above 25 in. Among the important herbaceous species in this zone are several grasses, such as Arizona bunch grass, *Festuca arizonica*, mountain bunch grass, *Muhlenbergia gracilis*, and a wide variety of herbaceous dicotyledons.

For more complete descriptions of these plant communities, reference may be made to Shantz and Zon ('24), and Hanson ('24).

In general, areas with dense shrubby growth were avoided. Except for this, plots were chosen to be as nearly representative of the major plant communities as possible. In all three zones, it was also possible to select more or less natural areas and some that had been more or less changed by grazing, lumbering, or fire. In nearly every case, the density of vegetation was rather low and in only one or two cases did it approach a sod, or similar complete ground cover. The density of herbaceous vegetation was lowest in the desert grassland and highest in meadow-like communities of the yellow pine zone.

The number of the sample series located in each of these zones was: Desert Grassland, 65; Intermediate, 9; Yellow Pine Forest, 24. The 98 sample series yielded a total of 3396 frequencies for the 1 sq. m. quadrats and 2420 for the 0.1 sq. m. quadrats. On the basis of the 1 sq. m. series, there was an average of 35 species for each plot. The average number for the 0.1 sq. m. series was 25. These species showed a wide range in frequency index as indicated in table III.

Of the total number of species found on the 1 sq. m. series, 28.7 per cent were not represented in the corresponding 0.1 sq. m. series, otherwise, the

TABLE III. *Distribution of frequency indices by classes*

Frequency index	Per cent of total	
	1 sq. m. series	0.1 sq. m. series
0	0.0	28.7
1– 5	39.9	29.2
6– 10	11.9	16.5
11– 15	7.3	6.1
16– 20	5.2	4.2
21– 25	4.4	2.9
26– 30	3.5	2.4
31– 35	2.9	1.8
36– 40	2.1	1.1
41– 45	2.2	1.5
46– 50	1.8	0.8
51– 55	1.8	0.8
56– 60	2.3	0.7
61– 65	2.0	0.6
66– 70	2.4	0.6
71– 75	2.0	0.7
76– 80	1.6	0.5
81– 85	1.6	0.2
86– 90	1.8	0.2
91– 95	1.9	0.2
96–100	1.3	0.2

proportional distribution is very similar. If the 0.1 sq. m. series includes only 71.3 per cent of the species in the 1 sq. m. series, the question may be raised as to whether or not the frequency index figures represent the total population for the 10,000 sq. m. plot. They do not include the entire population, but they do include the major portion. Check observations in each case showed that the majority of species were included and that only the rarer species were missed.

There has been considerable discussion as to the relative abundance of the individuals of various species in any given plant community as indicated by frequency index studies. Raunkiaer ('18) found that if the various species present be grouped into frequency classes of 20 each, designated as A, B, C, D, and E, representing frequency indices of 1–20, 21–40, 41–60, 61–80, and 81–100, the per cent of the total species falling in each class may be expressed as $A > B > C \gtreqless D < E$. Thus, 8078 frequency indices gave the ratio 53, 14, 9, 8, 16. Kenoyer obtained similar results on the basis of 1425 frequency indices from the region around Lake Michigan. He notes a tendency for Class A to be larger and Class E smaller than in Raunkiaer's study. He attributes this to the less stabilized condition of the communities studied. Kenoyer also notes that were the number of species is small, they tend to be confined to Classes A and E.

Hanson and Ball ('28) found that under deferred grazing the frequency index ratio of 62, 14, 7, 7, 10 approached those of Raunkiaer and Kenoyer, but that under continuous grazing there was an increase in Classes C and D, largely at the expense of Class E. Hanson and Love ('30), using quadrats of

different sizes, found that the percentage of species in Class A was always greatest but that the percentage in this class decreased with an increase in the size of the quadrat. An increase in the number of species falling in Class E, as compared to Class D, was shown for the 0.25, 2, and 3 sq. m. quadrats in a continuously grazed pasture and the 4 sq. m. quadrats in the pasture under deferred grazing.

In table IV, the distribution of the various species by frequency classes in the present study is compared to those obtained by Raunkiaer, Kenoyer, and Hanson and Ball.

TABLE IV. *Comparison of frequency indices by classes*

	Total number of frequency indices	Class percentages A	B	C	D	E
Raunkiaer	8078	53	14	9	8	16
Kenoyer	1425	70	12	6	4	7
Hanson and Ball						
Deferred pasture	42	62	14	7	7	10
Continuously grazed pasture	47	59	13	13	11	4
Arizona, meter	3396	64	13	8	8	7
0.1 meter [3]	2420	79	12	5	3	1
0.1 meter [4]	3396	85	8	4.	2	1

[3] Based on the frequency indices recorded for 0.1 sq. m. quadrats.

[4] Based on all frequency indices. Class A would include all frequency indices from 0–20.

The frequency indices included in the Arizona studies represent several conditions of grazing and protection from grazing, and variations in ecological conditions such as desert, grassland, and coniferous forest, but in all cases the density of vegetation is relatively low.

It would appear from these data that the ratio of frequency classes is not a constant for all conditions and all methods of obtaining frequency indices. The ratio is more of an expression of the relation between dispersal of individual plants and the size of quadrat used. Raunkiaer, working in a rather dense stabilized vegetation, obtained a certain ratio with 0.1 sq. m. quadrats. Kenoyer ('27, p. 344) found it necessary to increase the size of his quadrats to obtain the same ratio in certain communities. Hanson and Ball obtained the same ratio with 2 sq. m. quadrats in the less dense vegetation of Colorado. The ratios for the 1 sq. m. quadrats in the relatively sparse plant populations of Arizona approach the Raunkiaer ratio, but the 0.1 sq. m. quadrats show a steady decline in percentage, from an extremely large group in Class A, to 1 per cent in Class E. It is perfectly conceivable that the area of the quadrats could be altered so as to either reduce the percentage of species in Class E to zero, or, on the other hand, to throw all or almost all into Class A. Reducing the size of the quadrats will bring about an increase in the classes of lower frequencies and increasing the size of quadrats will increase the percentage

of species falling in the higher frequency classes. Gleason ('20) recognized this and suggested a formula for determining the size of quadrat which would include all species of a given abundance. Gleason ('29) showed further that these classes do not represent equivalent groups on the basis of abundance. This relationship is indicated in figure 1, which shows that the higher frequency index classes include a much greater range in abundance than do the lower. Gleason ('29) also pointed out that the ratio as expressed above will obtain only when quadrats are of such size as to include all species present in the five groups, and that " Raunkiaer's law is merely an expression of the fact that in any association there are more species with few individuals than with many. . . ."

The Relation between Frequency Index and Abundance under Average Field Conditions

It has been shown that with good random distribution, the frequency index offers a good measure of abundance. Mathematically, the method is sound, provided that the population examined is one in which the individuals are independently distributed at random in accordance with the law of chance. If

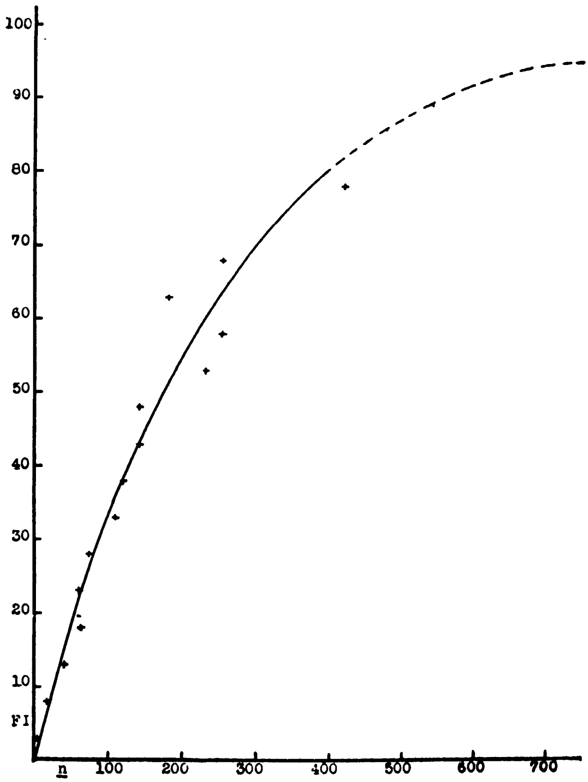

Fig. 2. Relation of frequency index to abundance for the 1 sq. m. quadrats.

the individuals of the various species are independently distributed at random, the relationships determined in the laboratory should hold in the field; if they are not distributed at random, the general principle might still hold within reasonable limits, provided that the irregularities are of such a nature as to be subject to mathematical treatment.

Many investigators, including Gleason ('20) and Arrhenius ('21), believe that in general the individuals of a given species represent a random distribution, while others, notably, Romell ('30), believe there is a tendency for over and under dispersal. Gleason ('20), while believing in random distribution,

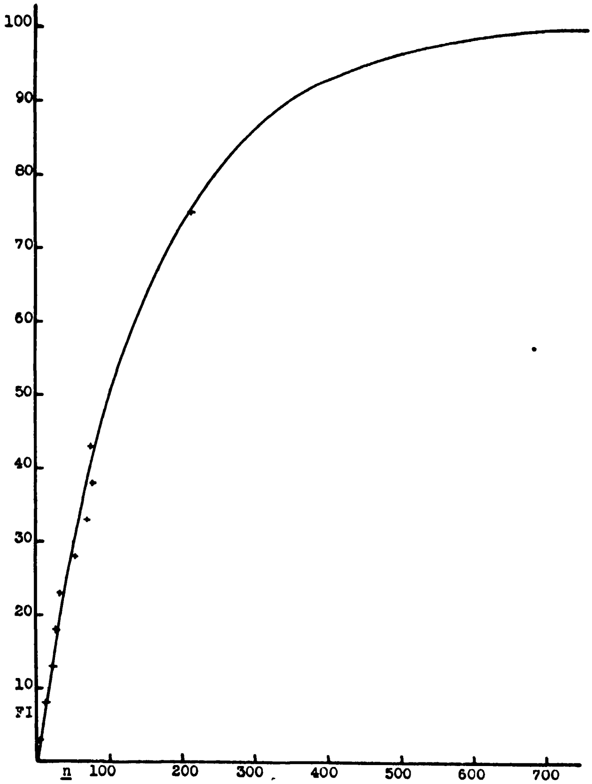

Fig. 3. Relation of frequency index to abundance for the 0.1 sq. m. quadrats.

does recognize irregular distribution in unstabilized communities and ('29) for plants propagated vegetatively. He ('20) also states that "It is not possible to draw any accurate conclusions as to the relation between theoretical and actual number of individuals, but in general, the theoretical number is one-fifth to two-thirds as large as the actual. . . ."

One of the objects of the present study was to determine if actual abundance could be calculated from frequency indices. The first step was to determine the degree of correlation between frequency indices and actual abundance

dance. On the basis of 298 counts, each representing the total abundance of a given species on 100 quadrats from representative plots, correlation ratios for the 1 sq. m. quadrats were found to be $\eta xy = 0.8553 \pm 0.0105$ and $\eta yx = 0.8302 \pm 0.0121$. The corresponding correlation ratios of the 0.1 sq. m. quadrats were $\eta xy = 0.8357 \pm 0.0122$ and $\eta yx = 0.8753 \pm 0.0095$. With such a high degree of correlation, it would appear that the relation between frequency index and abundance might be subject to mathematical treatment. When the curves for these relationships are plotted (figs. 2 and 3), it is seen that they have the same general form as that shown in figure 1, but that the slopes of the curves are not the same. However, in each case the experimental curve very closely approximates an equational curve such as that suggested by Gleason. In the case of the curve for the 1 sq. m. quadrats, there is a marked tendency for the frequency index values for any given abundance to fall below the equational curve for frequency indices between 70 and 100. There are not enough data available at the present time to determine whether this is due to some distributional factor or to errors in counting. For this reason, the upper portion of the curve is shown by a broken line.

The general trend of the curves representing the field data is toward a greater abundance of individuals for a given frequency index. In fact, for the 1 sq. m. series, the abundance indicated is 2.5 times as great for a given frequency index as that for a corresponding frequency index in the bead study, and the abundance for the 0.1 sq. m. series is 1.5 times that of the theoretical curve based on ideal random distribution. The curve equation in these cases becomes:

$$\mathrm{FI} = 1 - (0.99)^{\frac{n}{2.5}} \text{ for the 1 sq. m. series, and}$$

$$\mathrm{FI} = 1 - (0.99)^{\frac{n}{1.5}} \text{ for the 0.1 sq. m. series.}$$

Where n is the unknown, the equation becomes:

$$n = \frac{\mathrm{Log}\ (1 - \mathrm{FI})}{\mathrm{Log}\ 0.99} \text{ as applied to the bead results,}$$

$$n = 2.5 \frac{\mathrm{Log}\ (1 - \mathrm{FI})}{\mathrm{Log}\ 0.99} \text{ for the 1 sq. m. series, and,}$$

$$n = 1.5 \frac{\mathrm{Log}\ (1 - \mathrm{FI})}{\mathrm{Log}\ 0.99} \text{ for the 0.1 sq. m. series.}$$

The data obtained from the bead experiments representing random distribution indicate that the same basic equation could be used regardless of the size of the quadrat samples. They also indicate that the increase in abundance is proportional to the increase in area of the quadrat samples. In the results obtained from the field experiments, it is necessary to include a constant in the basic equation in order to construct suitable curves. This con-

stant is the same for all frequency index-abundance ratios as determined for a given quadrat size in a given type of vegetation, but is different for each different quadrat size and may vary with the type of vegetation under consideration. The above constants represent the average of 98 sample series located over a rather diverse vegetational range. All these plant communities have one thing in common, however, and that is that the vegetation is relatively sparse.

In order to determine the relation between abundance of the various species on the 1 sq. m. and 0.1 sq. m. quadrats, the correlation was determined, and the relation was found to be linear with a correlation coefficient $r = 0.8635 \pm 0.0103$, but instead of the ratio of abundance on the two areas being 1 to 10, it was approximately 1 to 7. It might be that this lowered ratio is due to deviations of insufficient number of samples and that the ratio should be 1 to 10. This does not seem to be probable, however. The deviations from the mean are large but not sufficiently large to account for such a difference. Furthermore, when abundance is predicted by frequency indices, using the equational curves, a close correspondence is found to this ratio; and when the ratio between the abundance on the 0.1 sq. m. series and the 1 sq. m. series is computed from these frequency indices, it is found to be 1 to 6.73. The explanation for a ratio of the number of individuals of approximately 1 to 7 on quadrats with a ratio of 1 to 10 in their respective areas is not readily apparent. With good random distribution in the bead experiments, the increase in number of individuals was directly proportional to the increase in area, but in the field the increase in the number of individuals is not directly proportional to an increase in area.

This difference might be due to over or under dispersal of individuals as pointed out by Romell ('30) provided that there was not a tendency for over dispersal and under dispersal to compensate when a large number of species are considered. Under the conditions of this experiment, irregular patches of bare ground were common, and it may be that the irregular distribution of the vegetation, alternating with these bare areas, would account for this lowered ratio. Further experiments are needed to furnish additional information before this problem can be definitely answered.

The Relation between Frequency Indices Obtained from Quadrats of Different Sizes

It has been pointed out previously in this paper that frequency indices vary in magnitude according to the size of quadrat used. Quadrats of different sizes will give entirely different ranges of frequency indices. The problem of the optimum size for quadrats has been considered by a number of investigators.

Raunkiaer ('09) tested quadrats ranging in size from 100 dm² to 1 dm² and decided that quadrats with an area of 0.1 sq. m. were most satisfactory.

Arrhenius determined by various calculations that the amount of deviation would be nearly inversely proportional to the area of the quadrat used, but that this larger deviation could be overcome by increasing the number of quadrats. He estimated that 200 tenth meter quadrats would give significant results. Gleason ('20) recognized the relation of size of quadrats to the frequency indices obtained, and gives formulae for calculating the size of quadrats necessary to obtain a quadrat which will include all the plants of a given frequency. He states that the optimum size is one in which there is a wide divergence of frequencies from 1 to 90 or even more. Kenoyer ('27) used quadrats varying in size from 0.1 sq. m. for dense herbaceous vegetation up to 100 sq. m. where only woody forms were considered. The size was adjusted so that a J-shaped curve was secured when the frequency indices were plotted according to the number falling in 5 classes (0–20, 21–40, 41–60, 61–80, 81–100).

Hanson and Love tested quadrats with areas of 0.25, 0.5, 1, 2, 3, and 4 sq. m. and decided that 1 sq. m. was the optimum size. They reached this decision largely because plotting the number of species against the size of the quadrat in square meters gave a curve with a tendency to flatten at 1 sq. m. This indicated that up to 1 sq. m. each addition in size of the quadrat would result in a considerable gain in the number of species included. The curve flattened out still more for 2 sq. m. but they concluded that when time was considered, the greatest efficiency would result from the use of 1 sq. m. quadrats.

Romell ('30) concluded that plants are not distributed at random and that very different results would be obtained by the use of quadrats of various sizes, and he recommended that 0.1 sq. m. be adopted as standard. On the other hand, Cain ('32) recommends that the size of the quadrat be adjusted to the purpose of the investigation and the character of the vegetation.

It follows, that if quadrats of different sizes are to be used by different investigators, the full value of such investigations will not be forthcoming unless there is some way of correlating the results obtained by the various investigators. It has already been shown that there is a high degree of correlation between the frequency indices obtained by quadrats of two different sizes under rather ideal conditions with beads. Under field conditions where there is a difference in the equation expressing the relation of frequency index for the 1 sq. m. and 0.1 sq. m. quadrats, the question might be raised as to whether or not a high degree of correlation existed. To determine this point, the correlation ratios were determined for 1511 paired frequencies ranging from 11 to 90 for the 1 sq. m. series and from 1 to 85 for the 0.1 sq. m. series. They were as follows: $\eta xy = 0.8840 \pm 0.00379$ and $\eta yx = 0.9092 \pm 0.00301$, indicating high positive correlation. Furthermore, when a curve is plotted to show the relation of the frequency indices of the 1 sq. m. quadrats to that of the 0.1 sq. m. quadrats (fig. 4), it is found that the curve is identical with that shown in figure 2 for predicting abundance from frequency index for the

1 sq. m. quadrats. That is, the relation between frequency indices for these two quadrat sizes is the same as the relation of the frequency index of the larger to its abundance divided by 10. This relationship was tested with the bead data and for a limited number of 0.1 sq. m. and 0.01 sq. m. quadrats, and for 10 sq. m. and 1 sq. m. quadrats, and was found to hold true in every case. It seems probable, therefore, that the relationship between frequency indices for quadrats is definite and subject to mathematical treatment. The relation

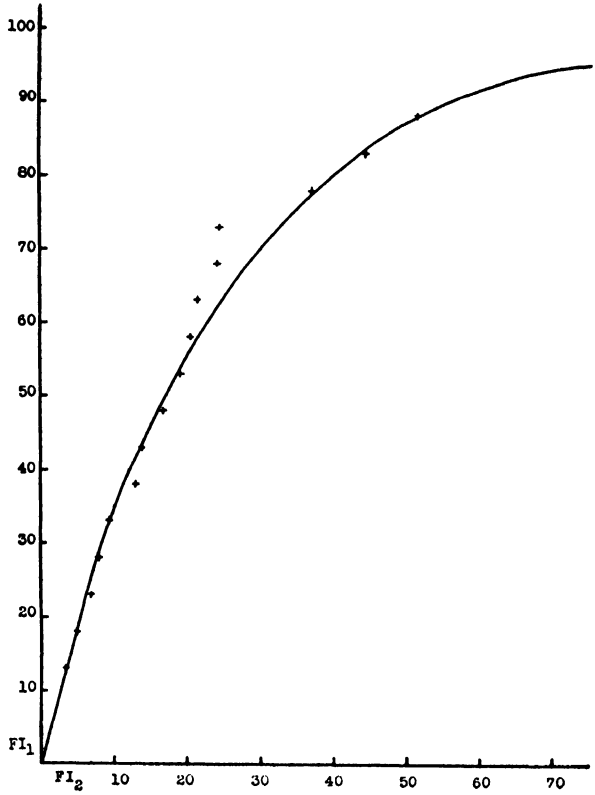

FIG. 4. Relation of frequency index for the 1 sq. m. quadrats to that for the 0.1 sq. m. quadrats.

of the frequency index of the smaller square to the abundance of the larger, where FI_1 and n_1 represent the frequency index and abundance respectively for the larger, FI_2 and n_2 the same quantities for the smaller, and a_1 and a_2 the area of the respective quadrats, may be expressed as:

$$FI_1 : n_1 = FI_1 : FI_2(a_1/a_2) \text{ or,}$$
$$n_1 = FI_2(a_1/a_2).$$

This relationship is shown in table V, where the first two columns represent the paired frequency indices from figure 4. The third column contains the

TABLE V. *The relation between the frequency index of 0.1 sq. m. quadrats and abundance for the 1 sq. m. quadrats*

Paired frequency indices from figure 4		Abundance	
FI_1	FI_2	n_1 from fig. 2	$FI_2 \times 10$
5	1	13	10
15	4	40	40
25	7	72	70
35	11	107	110
45	15	148	150
55	20	197	200
65	26	260	260
75	34	337	340
85	46	465	460
95	73	735	730

respective abundances for these frequency indices as read from figure 2. In the last column, the frequency indices for the small quadrat multiplied by 10 are given. These figures show a very close agreement throughout the entire range when the averages of a great many species are considered. Individual species on a single plot show varying degrees of deviation from this general trend, but such deviations are usually consistent for both the counted and estimated abundance values.

Prediction of Abundance Based on Frequency Indices Obtained from Quadrats of Various Sizes

As there is a high degree of correlation between frequency indices obtained by quadrats of various sizes, it is possible for the size to be adjusted to the character of vegetation and the purposes of the investigation. In some cases it may be that a general picture of the relative abundance of the various species is all that is desired. In other cases, as for example in range research, it is important to determine the differences in abundance of the most common species. In both of these cases quadrats should be used of such a size as to give the greatest range for the species under consideration.

To illustrate the differences in the range of frequency indices for different degrees of abundance, the paired frequency indices from figure 4 and the calculated abundance on 100 sq. m. are shown in the first three columns of table VI. The last two columns represent the difference in abundance divided by the differences in the respective frequency indices for the 1 sq. m. and 0.1 sq. m. quadrats.

In order to have a common basis for comparison, the abundance was computed on the basis of 100 1 sq. m. quadrats. As the n_1/FI_2 ratio, as shown above, is 10, the figures in the last column show a constant value approaching 10. The deviations are due to the inability to read the curves closer and also, because frequency indices were not carried into decimals.

For the smaller degrees of abundance, the ratio n/FI is much smaller for

TABLE VI. *Range in frequency indices for the 1 sq. m. and 0.1 sq. m. quadrats*

Paired frequency indices from figure 4		Abundance on 100 sq. m.	n/FI ratio	
1 sq. m.	0.1 sq. m.		1 sq. m.	0.1 sq. m.
5	1	13		
			2.7	9.0
15	4	40		
			3.2	10.7
25	7	72		
			3.5	8.8
35	11	107		
			4.1	10.2
45	15	148		
			4.9	9.8
55	20	197		
			6.3	10.5
65	26	260		
			7.7	9.6
75	34	337		
			12.8	10.7
85	46	465		
			27.0	10.0
95	73	735		

the 1 sq. m. quadrats but as the degree of abundance becomes greater, the n/FI ratio of the 1 sq. m. quadrats approaches that for the 0.1 sq. m., and somewhere between 75 and 85, the ratio of the latter becomes smaller than the former. As it is advantageous to have the n/FI ratio as low as possible, it would seem preferable to use a 1 sq. m. quadrat for all species with a frequency index on the 1 sq. m. quadrats of 80 or less. This represents an average abundance of about four individuals on each square meter. If more than an average of four plants are present on each square meter, a smaller quadrat would appear to yield more satisfactory results. Under the average conditions of the present study, 85 per cent of the species show a frequency index of 80 per cent or less.

Whether or not it would be worth while to use a smaller quadrat, would depend in part on the purpose of the investigation. In order to determine the relative numerical importance of the individual plants representing the species falling in the various classes, the number of individual plants which might be expected within each class on 100 1 sq. m. quadrats was computed on the basis of the average plant population. These figures based on the average percentages for all plots are shown in table VII.

TABLE VII. *Number of species and individual plants by frequency index classes*

Frequency index class	Number of species	Number of plants on 100 sq. m.	Per cent of total
1- 20	22.40	605	15
21- 40	4.55	400	10
41- 60	3.80	654	17
61- 80	2.80	832	21
81-100	2.45	1444	37
Total	35.00	3935	100

The number of individual plants was computed by multiplying the number of species within the class by the average abundance for the class. The greatest number of species is found in the lowest frequency class, but the average abundance of these species is low, so that only 15 per cent of the total number of individual plants are included in this class. The highest frequency class, even though it has the smallest number of species, includes more than a third of the total number of individuals. From a range research viewpoint, this highest class is very significant as it quite commonly includes the most important forage plants. Changes and variations in this class may also be of consisderable ecological significance. Other things being equal, variations in abundance within this class would be measured more accurately by the 0.1 sq. m. quadrats than the 1 sq. m. quadrats. The range in frequency indices of 20 for the 1 sq. m. for the relative abundance of the various species in this class, is contrasted with a frequency index range of 60 for the same species when based on the 0.1 sq. m. quadrats.

There is a considerable advantage in the use of a double frame for the determination of frequency indices. The two sets of frequency indices serve to some extent as a check on each other: the larger quadrats give a better differentiation of the less abundant species; the smaller quadrats give a better differentiation of the more abundant species; and finally, the frequency indices of the smaller frame, when multiplied by a suitable factor, give an approximation of the abundance of the various species found on the larger quadrats.

Conclusions

1. Under ideal conditions, there is a high degree of correlation between frequency index and abundance. Under field conditions, although the relationship between frequency index and abundance is somewhat altered, there is still a high degree of correlation. Under both conditions, abundance can be calculated for a given frequency index by means of the proper curve or equation.

2. There is a high degree of correlation between the frequency indices obtained simultaneously for 1 sq. m. and 0.1 sq. m. quadrats. Furthermore, the frequency index for 0.1 sq. m. quadrats multiplied by 10 approximates the abundance on the 1 sq. m. quadrats.

3. The 1 sq. m. quadrat gives the lowest *n*/FI ratio for the less abundant species, and 0.1 sq. m. quadrat gives the lowest for the more abundant species. The size of the quadrat used should be determined by the character of the vegetation and the purpose of the study.

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THE STATISTICAL THEORY OF POLLEN ANALYSIS [1]

FRED A. BARKLEY

University of Oklahoma

This paper represents an attempt to apply statistical analysis to the method of counting fossil pollen, in the hope of justifying or disqualifying the validity of the present method of pollen analysis. Inasmuch as the question frequently arises as to the validity of the method of sampling (*i.e.* the analysis of the sample represented on a slide), it seems timely that a statistical study of this method be made.

The purpose of present studies of peat pollens is to obtain indicators of past climates. In general when one finds a stratum containing a high percentage of pollen characteristic of any type of climate, it is concluded that that type of climate existed during the deposition of the stratum; where one finds an approximately equal percentage of pollen characteristic of two types of climate the inference is drawn that an intermediate type of climate existed during the deposition of the stratum; and where one finds a very low percentage of pollen characteristic of any type of climate, one concludes that that climate did not exist during the deposition of that stratum.

The question has been raised as to the number of grains that need to be counted in order to obtain a sufficiently reliable count for climatic interpretation. Sears ('30) counts 100 to 200, Erdtman ('31) 150, Lewis and Cocke ('29) 800, and Bowman ('31) 1000 to 1800 from each depth.

One practical test for the reliability of a set of data is to take two samples of the data, and obtain the coefficient of reliability [2] (*i.e.* the Pearson correla-

[1] Contribution from the Botanical Laboratory of the University of Oklahoma No. 24.

[2] The method used for obtaining a coefficient of reliability between halves of a pollen count was as follows: The types of pollen found were recorded in the first column. In the X-column the number of pollen grains of each type found in the first hundred count was recorded, and in the Y-column the number of pollen grains of each type found in the second hundred count was recorded. The value of the X-column was squared and placed in the fourth column, then the Y-value was squared and placed in the fifth column. The product of the X- and the Y-values was placed in the sixth column. The means (M) were obtained by summating each column and dividing by the number of types of pollen grains found in the counts of the slide. The coefficient of reliability (r), was obtained then, by substituting the values obtained by the above procedures, in the following formula:

$$r = \frac{MXY - (MX \cdot MY)}{\sqrt{MX^2 - (MX)^2}\sqrt{MY^2 - (MY)^2}}.$$

The standard error of the coefficient of reliability (σr) was obtained by substituting the values obtained for a given r, in the formula: $\sigma r = \frac{1 - r^2}{\sqrt{N}}$ (where N is the number of types of pollen grains in the count).

tion coefficient) between the two. The coefficient of reliability serves as an objective and impartial measure of the degree of reliability between two series of data. With the Brown "prophecy" formula [3] and an obtained coefficient of reliability for a given count, one may find the count required to obtain any other coefficient, or the coefficient that would be obtained from any other count. Table I illustrates the method used to obtain the coefficient of reliability and its standard error, and the application of the Brown "prophecy" formula.

TABLE I. *The calculation of the coefficient of reliability (r) by the gross score method, for the reliability between the first hundred grains of pollen counted (the x-count) and the second hundred grains counted (the y-count), in a low power count of slide 1031, and the calculation of the probable coefficient of reliability (r_p) for a count of a hundred and fifty grains against another hundred and fifty.*

Pollen type	X	Y	X^2	Y^2	XY
Juglans	2	1	4	1	2
Nyssa	14	15	196	225	210
Fagus	2	3	4	9	6
Cyperaceae	4	3	16	9	12
Betulaceae	13	7	169	49	91
Salix	3	3	9	9	9
Quercus	13	17	169	289	221
Unknown	5	6	25	36	30
Gramineae	8	6	64	36	48
Umbelliferae	2	2	4	4	4
Pinus	8	6	64	36	48
Castanea	2	2	4	4	4
Tsuga	7	10	49	100	70
Compositae	4	2	16	4	8
Tilia	1	2	1	4	2
Fraxinus	1	0	1	0	0
Ericaceae	2	7	4	49	14
Picea	2	1	4	1	2
Juniperus	1	0	1	0	0
Acer	1	0	1	0	0
Potamogeton	1	0	1	0	0
Abies	1	1	1	1	1
Nymphaea	2	3	4	9	6
Rumex	1	0	1	0	0
Ulmus	1	0	1	0	0
Celtis	0	1	0	1	0
Carya	0	1	0	1	0
Chenopodiaceae	0	0	0	0	0
Liquidambar	0	0	0	0	0
N = 29					
Total	101	99	813	877	788
Mean	MX = 3.48	MY = 3.42	MX² = 27.9	MY² = 30.2	MXY = 27.1

[3] A "prophecy coefficient of reliability" (r_p) was obtained by substituting the obtained coefficient of reliability in the Brown (Spearman) "prophecy" formula:

$$r_p = \frac{\overline{N}\ r}{1 + r(\overline{N} - 1)}$$ (where $\overline{N}$ is the number of times the count must be increased to obtain a given r_p).

$$r=\frac{MXY-(MX\cdot MY)}{\sqrt{MX^2-(MX)^2}\ \sqrt{MY^2-(MY)^2}}=.88,$$

$$\sigma r=\frac{1-r^2}{\sqrt{\bar{N}}}=.041,$$

$$r_p=\frac{\bar{N}\quad r}{1+r(\bar{N}-1)}=.916,$$

Theoretically a count of an infinite number of pollen grains is required in order to obtain a perfect correlation between halves of a count of pollen grains from a given sample of peat, so that the percentages of the pollen content are exactly the same between halves of the count. On the other hand the halves of a count of two or four pollen grains from such a sample shows no correlation (unless by accident) and does not give one an accurate picture of the pollen content. It is therefore necessary to find some satisfactory point between 0.0 and 1.0 correlation that is accurate enough for climatic interpretation and yet will not require much useless effort.

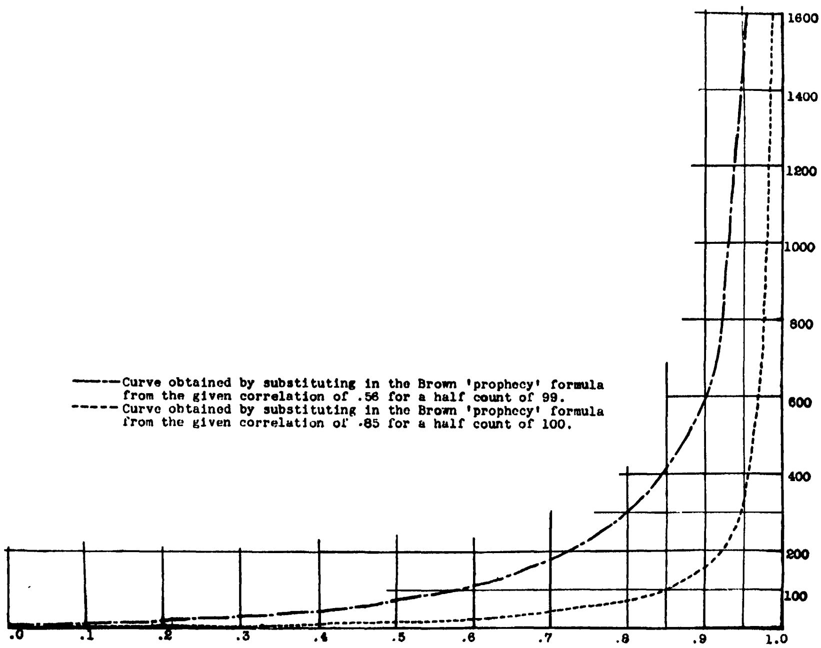

FIG. 1. Curves showing counts required for obtaining various coefficients of reliability.

A study of the frequency-correlation curve (fig. 1), shows that the curve begins to turn up rapidly between .6 and .7, requiring 1.50 as large a count to obtain a correlation of .7 as for a correlation of .6. To obtain an .8 correlation requires 1.77 as great a count as a .7. To obtain a count of .9 requires 2.25 as large a count as for an .8. However to go from a .90 to a .95

correlation requires a count increased 2.11 times that required for the .90. The point often chosen in other fields as sufficiently accurate for rather careful studies is about .90 (Ruch, page 433), as it shows a close correspondence between the halves yet is less than half as difficult to obtain as the only slightly more accurate .95 correlation.

There is no doubt that from a count correlating .90 with an equal count, one would obtain in any other equal sampling from a stratum a high percentage of the pollens giving a high percentage in the first, and a low percentage of pollens giving a low percentage in the first, and an intermediate percentage in the second when there is an intermediate percentage in the first.

Due to the variable rate of deterioration of various types of pollens, the original difference in pollen composition due to the variable amounts of pollen shed, the distance and pattern of scatter of pollen grains, and the differences due to the limited sampling of the peat sample placed on the slide for counting, anything finer than a relatively high, medium, or low percentage must be considered very cautiously, and minor fluctuations in percentages must not be considered with alarm.

Let us now study the counts required to obtain a .90 coefficient of reliability.

In order to study the relation between pollen counts, samples, approximately 1 cc. in size, were taken from the specimens near the center of three six-inch layers of peat from Bear Meadows Bog in central Pennsylvania. These were boiled in filtered 10 per cent potassium hydroxide, centrifuged, washed in filtered water, centrifuged, and mounted in glycerine jelly. Each slide was counted first under low power (making doubtful identifications under high power) until 200 grains had been counted. A 200 count of the slide was then made under high power. In both counts a $\times$ 10 eyepiece was used. In the low power count a $\times$ 10 objective was used, while for high power counts a $\times$ 45 objective was used. The coefficient of reliability was obtained for each count, the first half of each count being correlated against the second half (table II).

TABLE II. *A statistical study of pollen counts from a boring in Bear Meadows Bog*

Slide number	Coefficient of reliability between halves of a 200 count under high power	Count required to obtain a .9 coefficient of reliability between halves	Coefficient of reliability between halves of a 200 count under low power	Count required to obtain a .9 coefficient of reliability between halves	Number of types of pollen
1031	.94 ± .024	112	.88 ± .041	246	29
1032	.87 ± .046	268	.90 ± .044	200	25
1033	.72 ± .094	700	.78 ± .078	506	26
Average	.84	327 (164)	.85	317 (158)	27

In the low power counts a coefficient of reliability of .88 was obtained between counts of 100 pollen grains on slide 1031, of .90 for the same sized count of slide 1032, and of .78 for the same count of slide 1033; an average

correlation of .85. By applying the Brown "prophecy" formula one finds the counts required to obtain a .90 coefficient of reliability is 161, when, between 100 counts, the original coefficient of reliability is .85. Agreeing closely with Erdtman (page 400) and Sears' (page 210) estimate on the counts needed, a count of 175 to 200 grains should be considered sufficient.

Figure 2 is a graph showing the pollen composition of the two half counts

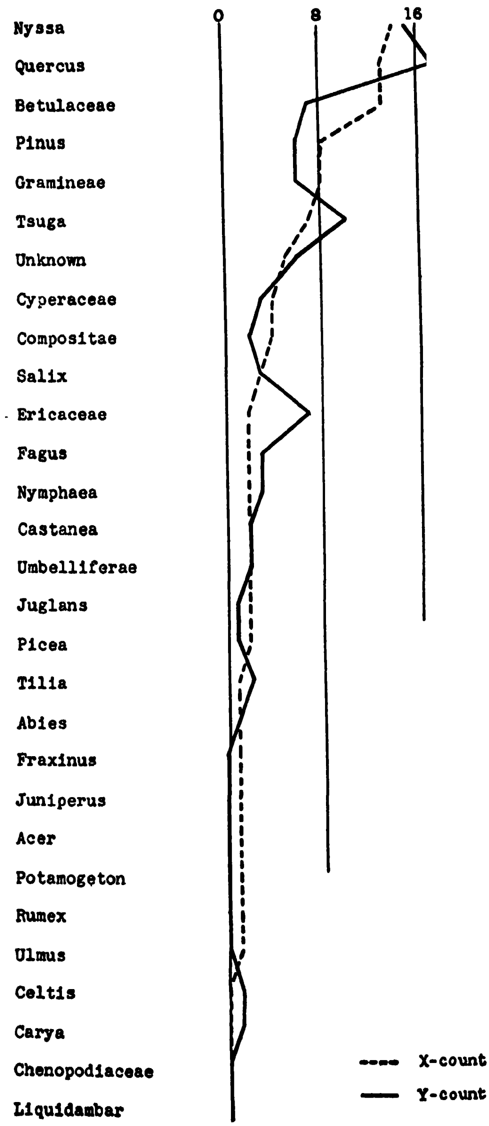

FIG. 2. Graph showing the pollen content of the halves of the low power count of slide 1031.

of slide 1031 when made under low power. It is seen from this that there is a close correspondence between the two counts. The coefficient of reliability for this count is .88 ± .041 (tables I and II).

In order to show the correspondence between samples in adjacent borings the author has correlated counts from corresponding layers of adjacent borings in Bucyrus Bog in Ohio (determined as corresponding by the same criteria used in other geological correlations). Table III, showing the coefficients of reliability obtained from this study, readily shows that one boring is only a mediocre sampling of the other. When this is taken into consideration, it would seem useless to obtain perfect counts from one side when at best that slide can be considered only a rough sampling of that stratum.

TABLE III. *A statistical study of pollen counts of correlated layers in adjacent borings in Bucyrus Bog*

Slide numbers	Correlation	Count required to obtain a .9 correlation of halves	Number of pollen types	Number of grains correlated	Correlation of 150 × 150 would obtain a correlation of
4 26	.89 ± .052	243	14	107 × 111	.92
9 28	.48 ± .250	2090	11	102 × 118	.55
10 29	.30 ± .302	3360	9	108 × 52	.44
Average	.56	1837	11	99	.64

By placing Bowman's curves (page 699) on ordinary graph paper for study, it is observed that there is only one case where there is a 2 per cent variation after the 450 count, and there is little significant shifting of relative percentages beyond the 200 count.

A glance at table II of the low and high power counts of Bear Meadows Bog shows that in the first slide the high power count (.94) was .06 better than the low power count, however the low power count of the second (.90) was .03 better than the high power count, and the third low power count (.78) was .06 better than the high power count. The average correlation between counts of 100 for the high power count was .84 while for the counts of the same slides under low power was .85.

From the type of material being studied, the correlations obtained between corresponding layers in adjacent borings, and the correlations obtained from counts on a single slide, the conclusion is that little or no validity accrues from counting above 200 pollen grains per slide. However, an increased validity would undoubtedly be obtained by averaging counts on samples from correlated layers in two or more adjacent borings. Further no significant advantage was observed in counting under low power rather than under high power, or vice versa.

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THE ANIMALS OF THE *LEMNA* ASSOCIATION

Minnie B. Scotland

N. Y. State College for Teachers, Albany, N. Y.

This is a study of the small animals in an association of one of the smallest flowering plants, *Lemna minor,* in the vicinity of Ithaca, N. Y. The dominant animal forms are naturally very small, ranging in size from a fraction of a millimeter to scarcely six millimeters in length. Yet, just as with large organisms, the destruction caused by them is compensated by the prolific growth of the plant.

The individual plants of *Lemna minor* are, as is well known, very small, flat, leaf-like discs, convex on the upper side and slightly concave underneath. A single water root dangles from the center of each green thallus and helps to maintain the equilibrium of the plant. Being a free-swimming hydrophyte, *Lemna minor* has many air cavities which make it buoyant. Stomata are scattered over the upper surface.

From April to October may be considered the active growing period of this species in the latitude of Ithaca, New York, with the peak of rapidity in growth occurring in July and August, when an entire pond may be blanketed with these small plants. Proliferation takes place in one plane, the lateral branches emerging from two clefts or pouches on the margin of the thallus. These new thalli are connected with the parent thallus by short slender stalks and are easily detached by a slight disturbance of the water. New centers of growth are thus established in the pond by the drifting apart of the disconnected offspring. In the fall, when conditions become less favorable for growth, lateral branches develop which lack air spaces and have plenty of reserve food. These winter buds sink to the bottom of the pond where they remain until the water becomes warm again the next spring. Then with the formation of air spaces, they begin their vegetative activities for the summer and rise to the surface. Propagation takes place also by the production of seeds from diminutive flowers (fig. 1).

Inasmuch as *Lemna minor* grows in quiet waters, it is not surprising that many filamentous forms of algae, as well as colonial types, are found among its roots and attached to the under surface of the thalli. Desmids and diatoms likewise abound. The liverwort, *Riccia natans*, and the spermatophytes, *Spirodela* and *Wolffia,* sometimes float about with the *Lemna.* Near the edges of ponds grow cat-tails (Typhaceae), bur-reeds (Sparganiaceae), and arrowheads (Alismaceae). Occasionally water-lilies (Nymphaeaceae), water cress (Cruciferae), *Elodea*, and *Ceratophyllum* associate themselves with the duckweeds (Lemnaceae).

In this *Lemna* association animals live either as obligates or as facultative residents. The one animal that finds in a single thallus an abundance of food to supply its needs throughout its entire life history is the ephydrid fly, *Lemnaphila scotlandae* Cress. This tiny fly, with iridescent wings, lays its ribbed, melon-shaped, yellowish eggs on the very edge of the upper surface of the *Lemna*, usually only one on a thallus. In size the egg measures .3 mm. long and .08 mm. at its greatest width and depth. The larva which emerges in

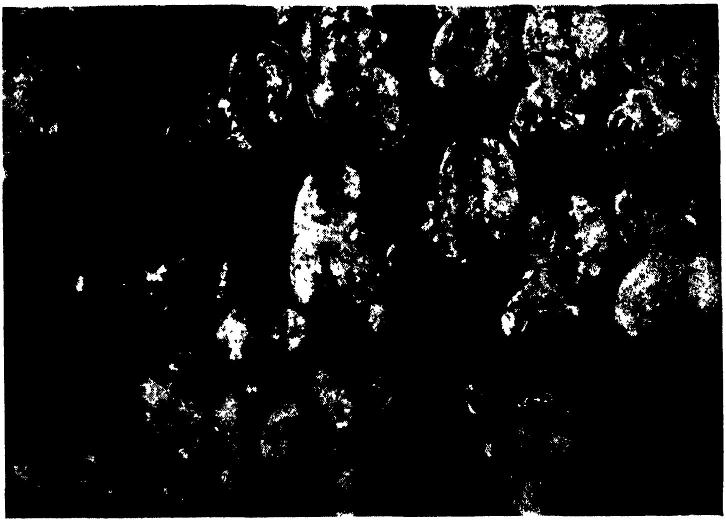

FIG. 1. *Lemna minor* in blossom.

two days splits the egg shell along a rib adjacent to the thallus and bores its way directly into the plant. Here it feeds on the food stored in the spongy tissue. After a day the first molting takes place within the thallus. There is merely a brief cessation in the feeding while the older larva with larger mouth hooks takes possession of the ready food supply. A third instar is reached after further eating and before ten days a golden brown puparium is formed. The adult fly emerges after four days, making the life history from egg to the imago just a little more than two weeks long.

Though the adult form has the power of flight, it makes little use of it. As soon as it has spread its wings it begins to eat out characteristic parallel channels in the upper surface of the thallus. This is accomplished by several rows of teeth that can be extended or retracted within the labellum. This gouging apparatus, surrounded by pseudotracheae, is very efficient. It makes the matter of food getting a simple one for the ephydrid. All the necessities of its existence are provided by this small plant.

A second obligate resident is the rhyncophorous beetle, *Tanysphyrus lemnae* Fab. This beetle, scarcely 1.2 mm. long and .6 mm. wide, chooses to lay its glistening, yellowish-white eggs singly in holes made in the upper surface

of the thallus. The holes are plugged with frass after each egg is laid. The mining larvae eat their way first in linear, and then in blotch-type mines between the upper and lower epidermal layers of the duckweed. Devastation of the spongy tissue proceeds so rapidly that many thalli are required to satisfy one individual's hunger during its larval period of two weeks. The adult also is ravenous, destroying many plants by gouging out round holes that often perforate the thalli (fig. 2).

Among the facultative residents there are some animals that use *Lemna* as

FIG. 2. *Lemna minor* infested by *Tanysphyrus lemnae*. The round holes are feeding punctures made by the adult. The linear ones and the blotches are leaf mines. One larva appears in a blotch mine at upper left.

a source of food. The aphid, *Rhopalosiphum nymphaeae* Linn., sucks the plant juices; the tiny collembolan, *Sminthurus aquaticus* Bourlet, eats morsels from the upper surface; and the larva of *Nymphula* (*Hydrocampa*) *obliteralis* Wlk. nibbles the edges of the thalli.

Since the individual *Lemna* plants are small, they serve these larger larvae also as material for case building. Whole thalli are used. The caddis worm, *Limnophilus combinatus* Walk., and the aquatic larva of *Nymphula* constructs its portable shelter mainly from the duckweed.

Lemna also offers to several facultative and temporary residents a place to lay their eggs. Beetles, especially *Hydroporus sp.*, glue their eggs singly on the roots. On the under side of the thalli the snails, *Planorbis* and *Lymnaea,* and the aquatic bug, *Trepobates pictus* H. S. attach their eggs in clumps of gelatine. Deep in the spongy tissue the water-strider, *Mesovelia bisignata* Uhler, oviposits, while in very small hemispherical depressions on the upper surface *Sminthurus aquaticus* lays its eggs.

With the profuse vegetative growth that characterizes *Lemna*, mats of the plants often cover large areas of still water. On the upper and lower sides of these mats many animals find support for crawling. The maze of roots serves as a hiding place for weaker individuals. Protozoans, rotifers, and crustaceans, as well as many aquatic bugs, swim in this entanglement of vegetation. *Hydra viridissima*, *Hydra vulgaris* and the flatworm, *Planaria maculata*, move about on the under side of the thalli in company with the snails and dark red water mites. The nymphs of damselflies and of mayflies crawl in this protective region while the beetle larvae, *Hydroporus*, *Tropisternus* and *Haliplus*, forage about. An occasional parasite, *Caraphractus cinctus* Wlk. (= *Polynema natans*) is in evidence, as a peril to eggs in such an association. On the upper side of a blanket of duckweed the adult carnivorous *Mesovelia bisignata* run rapidly; the tiny collembolans, *Sminthurus aquaticus* and *Podura aquatica*, skip about; and mosquitoes, both *Culex* and *Anopheles*, and flies of the families Dolichopodidae and Ephydridae stand or walk deliberately. A cricket nymph may jump from the bordering grass out on the duckweed of the pond, even nibbling on the edges of the *Lemna* thalli during its brief departure from its natural habitat.

The relationship between *Lemna* and the animals associated with it is a balanced one. In the case of the obligates, which develop from the egg to the adult entirely within the thallus, there is a very direct turn-over of plant substance into animal tissues. Even the carnivorous facultative residents owe their living to food supplied by the duckweed to the animals which they devour. *Lemna* also serves as an excellent protection and support for the eggs and for both the immature and the adult animal forms of its association. There is constant rapid replacement of new thalli by the plant.

Often these new plants establish themselves in new regions of the pond. Distribution is accomplished by the animals which they shelter. Swimming forms easily dislodge the plants, striking against their long roots, while the crawling animals aid in separating the lateral branches from the older thalli and in moving them about. *Lemna* likewise maintains its position in this society by the development of seeds. Here again the animal members of the association make this possible, for the scurrying insects on the blankets of *Lemna* pollinate the tiny imperfect flowers.

Summary

Animals associated with the duckweed, *Lemna minor*, in the vicinity of Ithaca, N. Y., may be divided into obligative residents and facultative residents. The obligates include the ephydrid fly, *Lemnaphila scotlandae* Cress., and the rhyncophorous beetle, *Tanysphyrus lemnae* Fab. The facultative residents include aphids, Collembola, caddis worms, aquatic beetles, aquatic bugs, mayflies, snails, etc. There are relations of mutual benefit between *Lemna* and many of its animal associates. The latter, while deriving food,

support, or protection from the plant, also help in its propagation and distribution.

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ADDITIONS TO THE FLORA OF HEART'S CONTENT, A VIRGIN FOREST IN NORTHWESTERN PENNSYLVANIA

H. J. Lutz

School of Forestry, Yale University

In 1930 the writer published in this journal an account of the vegetation of Heart's Content forest listing the plants then known to occur within the area. The stand is a remnant of the primeval forest which formerly covered much of northwestern Pennsylvania. A number of foresters and botanists, appreciating its ecological importance, have developed a lively interest in the area. Since 1928, when the initial studies were made, the place has been visited every summer and a number of additional species collected. The object of this paper is to record these species. The *Scirpus* sp. was immature but appeared to be *S. cyperinus;* it was impossible to collect flowers or fruit of either *Ribes rotundifolium* or *Crataegus tenella* hence the identification of these species remains tentative.

Some of the plants here reported seem to be recent invaders rather than natural components of the virgin forest. During the summer of 1929 cutting of immediately adjacent areas was completed, exposing the south and east sides of the virgin forest block. This exposure to sun and wind has certainly altered natural conditions within a considerable part of the forest and has made entry of a number of ruderals possible. A further factor in accounting for the recent arrivals seems to be the increasing use of the area by the public. Among the species which represent recent arrivals in the area are *Dactylis glomerata, Agrostis alba, Populus tremuloides, P. grandidentata, Rumex acetosella, Polygonum acre, Phytolacca decandra, Lysimachia quadrifolia, Solanum dulcamara, Bidens discoidea, Erechtites hieracifolia,* and *Hieracium aurantiacum.*

Plants occurring only in the grazed portion of the forest are not included. Information on such species may be obtained from an earlier paper by the writer.

Acknowledgment is made to Agnes Chase for identifying the grasses; to E. C. Leonard for identifying the Carices; to Ernest J. Palmer for identifying the Crataegus; and to Alexander Gershoy for identifying the Violas.

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TABLE I. *Additional species collected in Heart's Content forest*

Species	Relative abundance[1] Hemlock-beech association	Hemlock consociation
Phegopteris polypodioides Fée.	R	
P. dryopteris (L.) Fée.	R	
Asplenium filix-femina (L.) Bernh.	R	
Glyceria melicaria (Michx.) Hub.		R
G. nervata (Willd.) Trin.	R	
G. striata (Laur.) Hitchc.	R	R
Poa saltuensis Fernald & Wiegand.	R	
P. cuspidata Nutt.	R	
Dactylis glomerata L.	R	
Agrostis alba L.		R
A. perennans (Walt.) Tuckerm.	R	R
A. perennans var. *elata* (Pursh.) Hitchc.		R
Cinna latifolia (Trev.) Griseb.	R	
Panicum latifolium L.	R	
Scirpus sp. (*S. cyperinus* (L.) Kunth. ?)		R
Carex stipata Muhl.	R	
C. trisperma Dewey.	R	R
C. crinita Lam.		R
C. prasina Wahlenb.		R
C. scabrata Schwein.		R
C. baileyi Britton.		R
C. laxiculmis Schwein.	R	
C. laxiflora Lam.	R	
C. leptonervia Fernald.	R	
C. debilis Michx.	R	R
C. folliculata L.	R	
C. intumescens Rudge	R	
Juncus effusus L.		R
J. tenuis Willd.	R	R
Luzula campestris (L.) DC.	R	
L. campestris var. *bulbosa* A. Wood.	R	
Trillium undulatum Willd.	C	R
Populus tremuloides Michx.	R	
P. grandidentata Michx.	R	
Rumex acetosella L.		R
Polygonum acre HBK.		R
Phytolacca decandra L.	R	
Ranunculus recurvatus Poir.	R	
Cardamine pennsylvanica Muhl.	R	R
Chrysosplenium americanum Schwein.	R	
Ribes rotundifolium Michx. (?)	R	
Crataegus tenella Ashe. (?)	R	
Polygala paucifolia Willd.	R	
Viola papilionacea Pursh.	R	
V. incognita Brainerd. (approaching *V. blanda* Willd.)	R	
V. hastata Michx.	R	
V. canadensis L.	R	
Aralia racemosa L.	R	
Osmorhiza claytoni (Michx.) Clarke.	R	
Rhododendron canescens (Michx.) G. Don.	R	
Lysimachia quadrifolia L.	R	
Solanum dulcamara L.		R
Veronica officinalis L.	R	
Conopholis americana (L. f.) Wallr.	R	
Eupatorium urticaefolium Reichard.		R
Aster divaricatus L.	R	R

[1] Abundance is indicated as follows: C = common; R = rare.

TABLE I. (*Continued*)

Species	Relative abundance [1] Hemlock-beech association	Hemlock consociation
A. prenanthoides Muhl.	R	
Bidens discoidea (T. & G.) Britton.		R
Erechtites hieracifolia (L.) Raf.	R	
Senecio aureus L.		R
Prenanthes trifoliolata (Cass.) Fernald.	R	
Hieracium aurantiacum L.	R	

[1] Abundance is indicated as follows: C = common; R = rare.

TEMPERATURE STUDIES IN A COTTON FIELD, PRESIDIO, TEXAS, 1932[1]

L. C. Fife

U. S. Bureau of Entomology
in cooperation with the
Texas Agricultural Experiment Station

Introduction

Since temperature has a decided influence upon the activities and development of the pink bollworm (*Pectinophora gossypiella* Saunders), a study of this factor becomes of importance in helping to explain the relation of the habits and development of this insect to its environment.

The pink bollworm, during its growth from the egg to the adult, spends parts of its developmental period in several different micro-climates. For example, most of the eggs are laid under the boll involucres. After hatching, the young larva enters a green square or boll, in which it completes its feeding period. The short-cycle larva, after completing its feeding, usually tunnels an exit hole through the boll, drops to the ground, and spins a silken cocoon in the surface litter or in the soil, in which to pupate. When squares are infested, the larva may leave the bloom; or, if not fully developed at this time, remain in the old bloom, which drops to the ground after a few days. Most of the long-cycle larvae remain in the seed of open bolls. The moths, after emerging from their pupal cases, seek seclusion in the cracks of the soil during the day, but at night they become active and fly in and among the cotton plants.

In studying the life history and development of the pink bollworm in the cotton field, green squares and bolls were artificially infested with newly hatched larvae and then covered with transparent cellophane bags in order to prevent outside infestation. Since it was early discovered that the transparent cellophane bags caused an increase in air temperature inside the bag, it became important to know what effect the bag had upon the temperature inside the bolls or squares where the larvae were feeding. It also was necessary to find the relation of temperatures inside of the bolls and squares in the cellophane bags to the temperatures in those that were not covered with the bags and to air temperatures in the shade as recorded by a field thermograph in a weather bureau instrument shelter.

[1] This work was done under the direction of Dr. F. A. Fenton, Senior Entomologist, Division of Cotton Insects of the U. S. Bureau of Entomology and the author wishes to acknowledge the many valuable suggestions and criticisms received.

Methods

Temperatures were taken by the thermocouple method, using a potentiometer of an automatic reference cold-junction compensator type. Number 32 gauge, double covered constantan and copper thermocouple wires were used, which were enclosed in small rubber tubing. The thermo-electric junctions were enclosed in thin glass tubing which was drawn out to a small point, the glass serving as protection to the junction. The end of the glass tubing away from the thermo-electric junction was entirely closed with sealing wax. Temperatures under the boll involucre were taken by using bare thermocouple wires at the thermo-electric junction. Ten thermocouples were used, which were connected through a rotary switch to the potentiometer. The instruments were mounted on a table which was placed under a shelter made of a wood framework covered by a heavy tarpaulin.

Since, with the exception of the surface soil, no important night or cloudy weather temperature differences were found between the different micro-environments, the following discussion relates only to the temperatures taken in these different micro-environments during the day, *i.e.*, between 8 A.M. and 7 P.M. The average deviations or departures from the mean diurnal shade air temperatures were based on an average of six readings. These were taken at 8 A.M., 10 A.M., 12 noon, 2 P.M., 5 P.M., and 7 P.M.

Shade air temperatures were recorded by a thermograph in a weather bureau instrument shelter. The shelter was placed on the ground and it was shaded by the cotton plants during the course of these experiments. This instrument therefore recorded the temperatures about 10 inches above the ground. Temperatures in direct sunlight were only taken by the thermocouple method and therefore do not necessarily represent those in direct sunlight but can be used as a means of comparison of sun air temperatures in the open and in a cellophane bag.

Results

By taking the temperatures inside of many green bolls and squares, under the boll involucres, in the seed of open bolls, etc., at the same hour during the day, it was found that the principal factor causing temperature variations in these different micro-climates was the extent of their exposure to the direct rays of the sun. Also temperatures in bolls and squares did not vary with depth or with the size and age of the bolls or squares, when the periods of their exposure to the direct rays of the sun were equal. The temperatures in large bolls in the sun averaged 97.8° F., in large bolls partly in the shade 93.2° F., and in large bolls entirely in the shade 89.4° F. The shade air temperature at this time was 89.6° F. These records represent averages from a series of readings which are not recorded in the tables accompanying this report.

Temperatures in Different Micro-environments in a Cotton Field

The actual temperature readings in different environments in a cotton field are shown in table I and graphically illustrated in figures 1 and 2. These temperatures were taken simultaneously and therefore comparisons can be made both horizontally and vertically. The variability in each of the micro-

Table I. *Temperature readings in different environments in a cotton field during the day, Presidio, Texas, Aug. 22–28, inclusive, 1932*

Location of the thermocouple	Mean temperature at—						Day mean temperature	Maximum temperature
	8 A.M. (6 readings)	10 A.M. (6 readings)	12 noon (6 readings)	2 P.M. (6 readings)	5 P.M. (7 readings)	7 P.M. (1 reading)		
Boll in cellophane bag	86.7 [1] 73.9	103.3 82.9	100.6 87.4	102.1 93.4	98.3 90.7	88.7 86.0	96.6 85.7	108.5 95.0
Boll not in cellophane bag	78.4 76.3	93.9 81.1	93.9 82.6	97.7 88.9	96.3 86.7	86.0 85.1	91.0 83.4	101.3 91.4
Under the boll involucre	76.3 74.1	90.1 81.1	90.0 84.6	93.6 87.4	91.4 85.8	85.1 79.7	87.7 82.1	95.0 89.6
Inside of seed in an open boll	79.1 77.4	102.9 82.2	106.2 84.9	110.1 91.2	101.0 92.3	86.0 79.7	97.5 84.6	124.7 99.2
Open [2] air	77.2 73.9	89.0 83.3	89.8 84.4	93.3 88.0	91.1 86.9	79.0 81.2	86.6 82.9	95.0 90.5
Air in cellophane bag in the sun [2]	81.5	94.0	96.3	100.0	98.7	84.0	92.4	105.0
Soil surface in the shade	70.7	75.0	77.2	81.0	80.7	77.0	76.9	84.0

[1] Upper figures of double brackets in columns represent temperatures taken in the sun; lower, those taken in the shade. Comparisons can be made both horizontally and vertically.
[2] Temperatures recorded do not represent those of the air in direct sunlight but can be used as a means of comparison of sun air temperatures in the open and in a cellophane bag.

climates was found to be greater during the middle of the day. This doubtless was to be expected, since differences in the exposure during the hours of high light intensity would be more important and the relative differences in the transpiration rates would be more marked. By referring to figures 1 and 2 and table I, it will be seen that the environment having the lowest mean temperature was the soil surface in the shade, the peak being reached at 2 P.M. when the temperature averaged 81° F. In contrast, the environment having the highest mean temperature was inside of the seed in an open boll. Here the peak was also reached at 2 P.M. when the temperature averaged 110.1° F. The mean temperature of the other environments came in between these two. It will be noticed that most of the time, with the exception of the soil surface temperatures in the shade and those under the boll involucre in the shade, all environments were warmer than standard shade air temperatures.

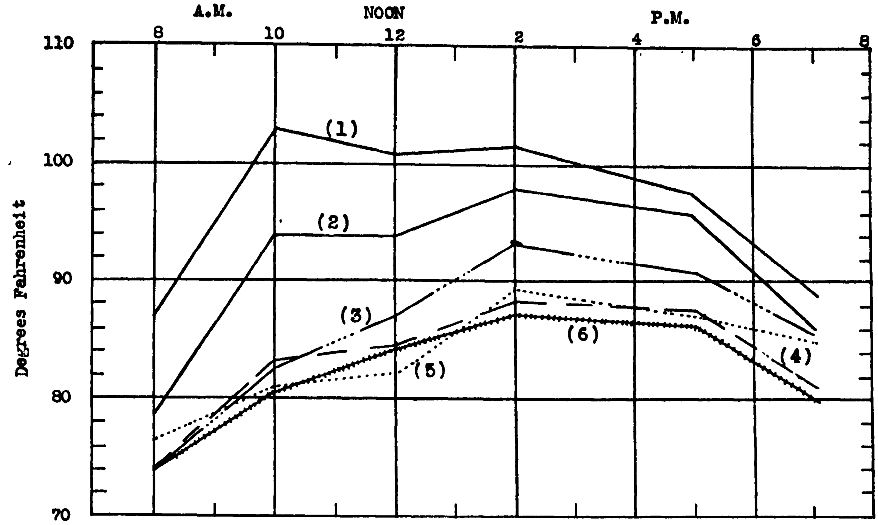

FIG. 1. Time-temperature curves showing a comparison of temperatures in different environments in a cotton field. Presidio, Texas. Aug. 22 to 28, inclusive, 1932. (1) Boll in cellophane bag in the sun. (2) Boll in the sun. (3) Boll in cellophane bag in the shade. (4) Shade air temperature. (5) Boll in the shade. (6) Under the boll involucre in the shade.

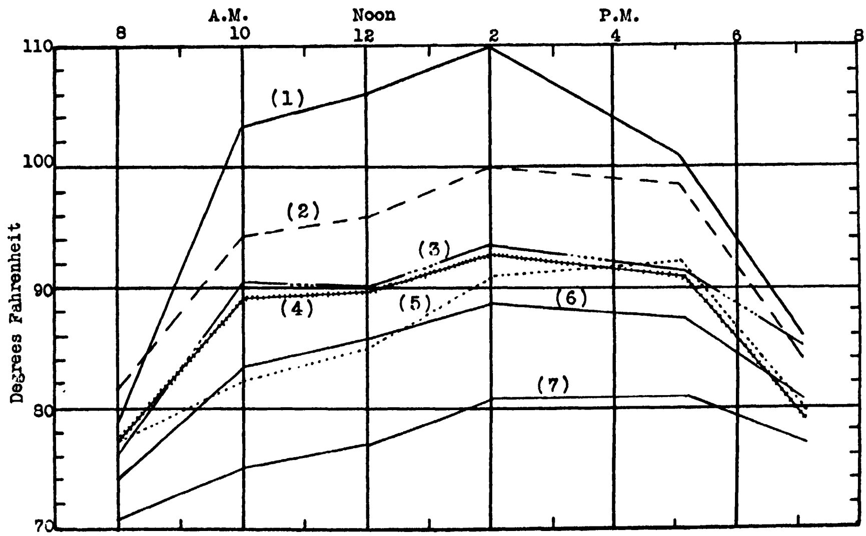

FIG. 2. Time-temperature curves showing a comparison of temperatures in different environments in a cotton field. Presidio, Texas. Aug. 22 to 28, inclusive, 1932. (1) Inside of seed in an open boll in the sun. (2) Air temperature in cellophane bag in the sun. (3) Under the boll involucre in the sun. (4) Air temperature directly in the sun. (5) Inside of seed in an open boll in the shade. (6) Air temperature in the shade. (7) Soil surface in the shade.

Temperature Departures in Green Bolls During the Day (8 a.m. to 7 p.m.)

The departure of temperatures in bolls on the cotton plant during the day from diurnal shade air temperatures is shown in figure 3. The data for the different micro-environments as shown in this figure and also table II, are based upon the average departure of their temperature readings from diurnal shade air temperatures at 8 a.m., 10 a.m., 12 noon, 2 p.m., 5 p.m., and 7 p.m.

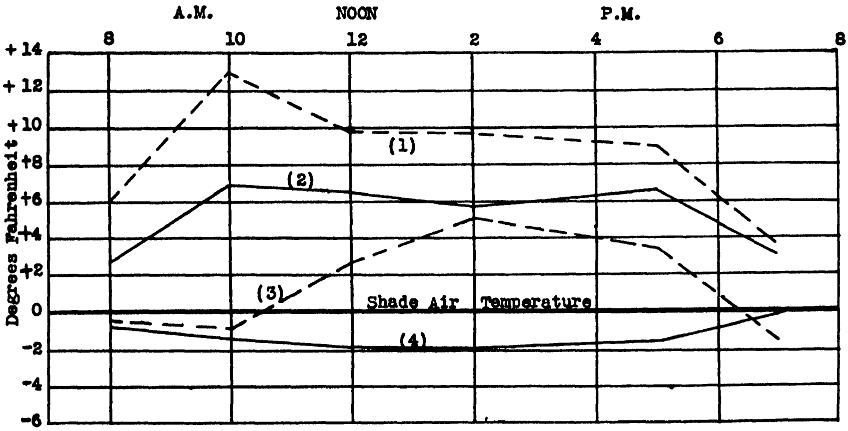

Fig. 3. Departures of temperatures of different environments on the cotton plant from shade air temperatures. Presidio, Texas, 1932. (1) Boll in cellophane bag in the sun. (2) Boll in the sun. (3) Boll in cellophane bag in the shade. (4) Boll in the shade.

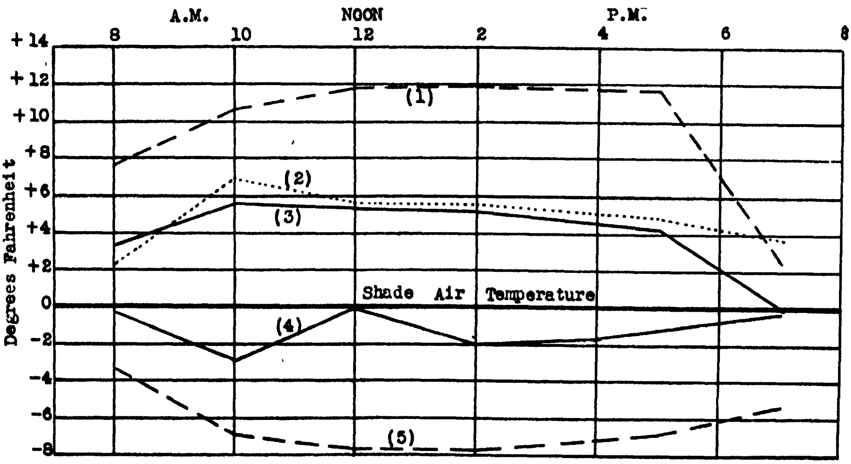

Fig. 4. Departures of temperatures of different environments on the cotton plant from shade air temperatures. Presidio, Texas, 1932. (1) Air temperature in cellophane bag in the sun. (2) Under the boll involucre in the sun. (3) Air temperature directly in the sun. (4) Under the boll involucre in the shade. (5) Soil surface in the shade.

They were taken over periods ranging from 6 to 20 days duration and over different periods of time. Therefore it is impossible to compare the different columns in table II vertically. In the last column are given the departures at maximum temperatures, and these no doubt also represent the maximum departures.

The results show that the shade air temperatures were not an accurate

TABLE II. *Departures of temperatures in different environments on a cotton plant from diurnal shade air temperatures, Presidio, Texas, 1932*

Location of the thermocouple	Number of readings	Mean temp. recorded by thermocouple[1] (° F.)	Simultaneous mean air temp. in the shade (° F.)	Departure of mean thermocouple temp. from mean air temp. in the shade (° F.)	Departure of max. thermocouple temp. from max. air temp. in the shade (° F.)
Square in cellophane bag	90 27	93.9 90.1	90.7 92.0	+3.2 −1.9	−0.9 −3.6
Square not in cellophane bag	63 63	92.8 89.7	90.2 90.2	+2.6 −0.5	+3.6 −8.1
Boll in cellophane bag	130 56	95.3 85.6	85.2 84.6	+10.1 +1.0	+18.0 +4.5
Boll not in cellophane bag	56 101	90.4 86.2	84.7 87.4	+5.7 −1.2	+10.8 −8.1
Under the boll involucre	32 83	87.7 85.7	82.9 87.0	+4.8 −1.3	+4.5 −3.6
In the seed of an open boll	64 32	97.5 84.6	82.9 82.9	+14.6 +1.7	+34.2 +9.0
Open air in the sun[2]	32	86.6	82.9	+3.7	+4.5
Air in cellophane bag in the sun[2]	32	92.4	82.9	+9.5	+14.5

[1] Upper figures of double brackets represent temperatures taken in the sun; lower, those taken in the shade. Comparisons can only be made horizontally.

[2] Temperatures recorded do not represent those of the air in direct sunlight but can be used as a means of comparison of sun air temperatures in the open and in a cellophane bag.

index to temperatures of bolls in the sun or shade. In the sun the boll temperature was always higher than the shade air temperatures, the average departure being + 5.7°, whereas in unbagged bolls in the shade it was always lower, the average departure being — 1.2°. Temperatures of bolls in the sun averaged 6.4° higher than those of bolls in the shade.

When bolls were covered with cellophane bags, the temperatures were further increased over those in the unbagged bolls, but the differences were less marked in the shade than in the sun. Temperatures in bolls in cellophane bags in the sun averaged 10.1° higher than shade air temperature, 5° higher than the temperature of unbagged bolls in the sun, and 9.8° higher than the temperature of bagged bolls in the shade. Temperatures of bolls in cello-

phane bags in the shade averaged 1° higher than shade air temperatures and 1.6° higher than the temperatures of unbagged bolls in the shade.

Temperature Departures under Boll Involucre, Seed of Open Bolls, and Surface Soil during the Day (8 a.m. to 7 p.m.)

The departure of temperatures in other different environments in a cotton field from air temperatures in the shade is shown in figure 4 and table II. These data were secured and calculated in the same manner as previously described. The temperature under the boll involucre in the sun during the day averaged 4.8° higher than shade air temperature and 5.6° higher than temperatures under the boll involucre in the sade. Temperatures under the boll involucre in the shade averaged 1.3° lower than air temperature in the shade.

The departures of the temperature in seed in an open boll from temperatures of other micro-environments are shown in tables I and II. It is seen that the temperature in the seed of an open boll in the sun averaged 14.6° higher than shade air temperatures and 12.9° higher than temperatures in the seed of an open boll in the shade. Temperatures in the seed of an open boll in the shade averaged 1.7° higher than shade air temperatures.

Surface soil temperatures in the shade under the plants were always lower than shade air temperatures, the deviation depending upon the amount of moisture at the soil surface. They averaged 6.6° lower than shade air temperatures. The air temperature in a cellophane bag was always higher than the air temperature directly in the sun, the day average deviation being 5.8° (fig. 4).

Temperature Departures in Squares During the Day (8 a.m. to 7 p.m.)

With one exception, temperatures in squares show practically the same results as have been shown for the temperatures in bolls, except that deviations were not so large (fig. 3 and table II). Temperatures in squares in the sun averaged 3.1° higher than those in squares in the shade and 2.6° higher than shade air temperatures. Squares in the shade averaged 0.5° lower in temperature than shade air temperatures.

When the squares were covered with cellophane bags, the temperatures were further increased over those in the unbagged squares, but the differences were less marked in the shade than in the sun. Temperatures in squares in cellophane bags in the sun averaged 3.2° higher than shade air temperatures and 1.4° higher than temperatures in unbagged squares in the sun. Bagged squares in the shade, however, averaged 1.9° lower in temperature than shade air temperatures, this being the exception already noted. The temperatures in the bagged squares in the shade averaged 0.5° higher than those in unbagged squares in the shade.

Conclusions

1. Diurnal shade air temperatures, as recorded by a field thermograph in a weather bureau instrument shelter, were not an accurate index to temperature in squares or bolls, under the boll involucre, in the seed of open bolls, or on the soil surface.

2. Direct sunlight greatly influenced the temperatures in squares and bolls, under the boll involucre, and in the seed of open bolls, increasing the temperatures in all cases.

3. The presence of a perforated cellophane bag over the square or boll increased the temperatures in these fruiting forms, whether in the shade or not, but the differences were greater in the sun and were greater in bolls in cellophane bags than in squares in cellophane bags.

4. Temperatures in bolls in cellophane bags in the shade during the day were higher than shade air temperatures, while in squares in cellophane bags in the shade the temperatures were lower.

5. The surface soil temperatures in the shade were always lower than the shade air temperatures, the deviation depending upon the amount of moisture at the soil surface.

6. Temperatures in green squares or bolls, under the boll involucre, or in the seed of open bolls tended to be equalized at night (8 P.M. to 7 A.M.) or during cloudy weather and were practically the same as air temperatures as recorded by the field thermograph.

7. The variability in each of the micro-climates was found to be greater during the middle of the day. This doubtless was to be expected, since differences in the exposure during the hours of high light intensity would be more important and the relative differences in the transpiration rates would be more marked.

8. The rather striking differences in the temperatures in the different micro-climates of the cotton plant clearly show that air temperatures as recorded by a field thermograph, even in a location close to the insect, do not give a true picture of the temperature conditions under which the insect is developing.

THE PLANT LIFE OF RUSSIAN LAPLAND

William Seifriz

University of Pennsylvania

The Kola Peninsula or Russian Lapland lies within the Arctic Circle some 750 miles north of Leningrad (fig. 1). It is bounded by the White Sea on the south and the Arctic Ocean on the north, thus extending from latitude 66° N. to about latitude 69° 5′ N., the north-western corner nearly reaching latitude 70° N. From west to east the Peninsula extends from Finland, at longitude 30° E., to the strait of the White Sea, at longitude 41° E. The northern part of the Peninsula may be reached by a forty-two hour rail journey from Leningrad to Murmansk, the northern terminal of the road, passing through the much older town of Kóla. Fourteen miles north of Murmansk lies Alexandrovsk, the most northern village of the Peninsula, and six miles more bring us to the open shores of the Arctic Ocean near which lies the Island of Kildin. In the center of the Peninsula are the Hibini Mountains, extending eastward from Lake Imandra. The Mountains have now become known to all Russians because of the recent discovery of valuable deposits of apatite (phosphorus ore).

This article has to do with the plant life of the two regions of the Hibini Mountains known as Tachtarvumchorr and Kukisvumchorr, and of the Island of Kildin.

On the east shore of Lake Imandra is the small settlement of Hibini [1] with a government agricultural experiment station (fig. 2). Less than a mile from the lake shore rise the Tachtarvumchorr Mountains. Ten miles south from Hibini is the station Apatíti from which a small railroad goes eastward to the new and rapidly growing town of Hibinogorsk on Lake Vudyavr. Four miles to the north, beside Small Lake Vudyavr, is the experimental station of the National Academy of Science of Leningrad. The mountains of this region are more majestic than those of Hibini. The panorama, though bleak, is truly a fine one. Glaciers are not present as the mountains are not sufficiently high, the maximum altitude being under 4000 feet. The climate of Lake Imandra and the Hibini Mountains is not as severe as one might expect from their arctic situation. The usual winter temperature is about — 10° C. (14° F.) though — 40° C. may be reached. Snow attains an average maximum depth of two meters. Summer temperature is about 15° C. Rains

[1] Hibini is usually written with a K or C as the initial letter, *Khibini,* probably in an attempt to obtain an English spelling which will give a pronunciation similar to the Russian.

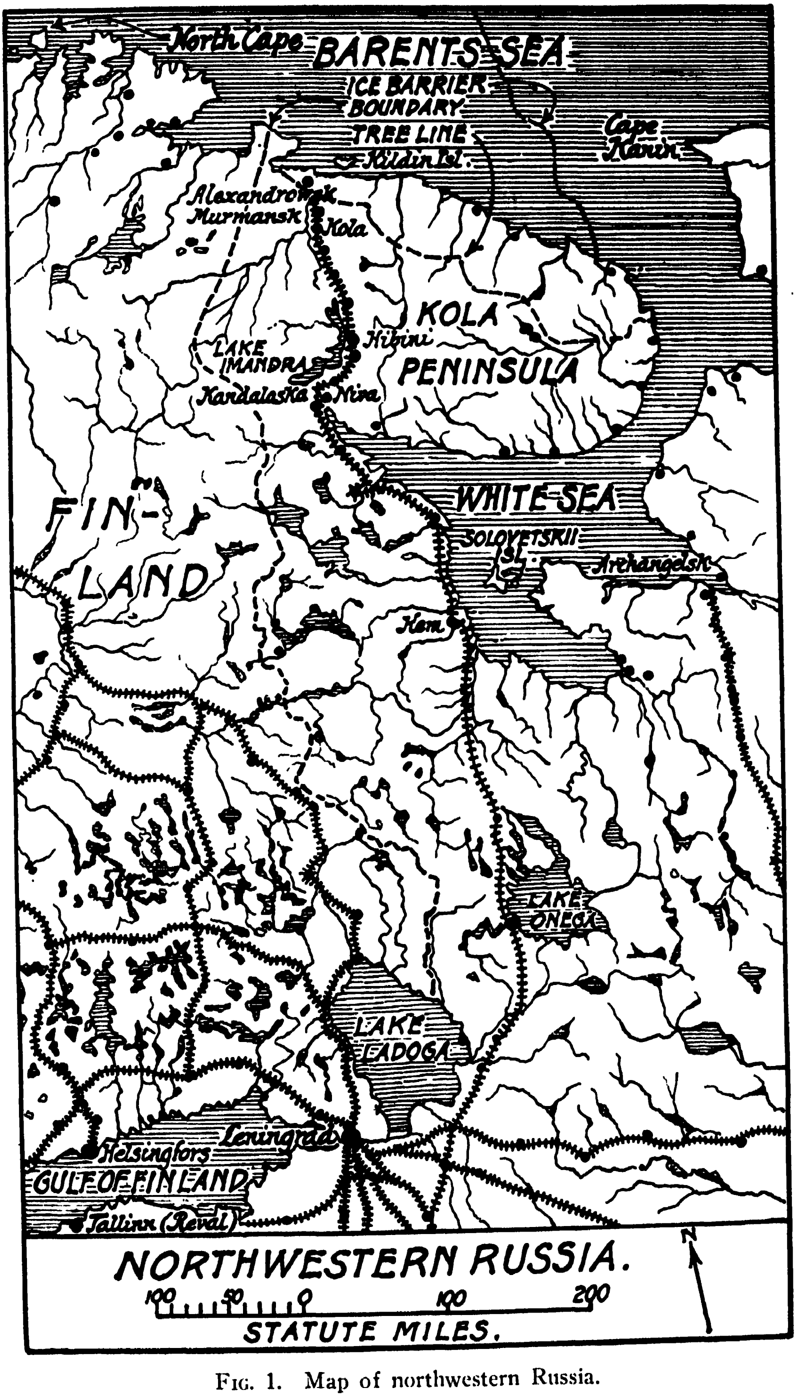

FIG. 1. Map of northwestern Russia.

and chilling winds are frequent, interrupted by a month of uncomfortably warm weather in summer. Daylight, or twilight, is perpetual from April to September.

Three Russian botanists, temporarily or permanently stationed in these regions, were of great help in the planning of trips and in the final identification of the plants collected; they are Johann Eichfeld, Director of the Hibini Station, George M. Kreps, Keeper of the Imandra Game Reserve, and Vlad-

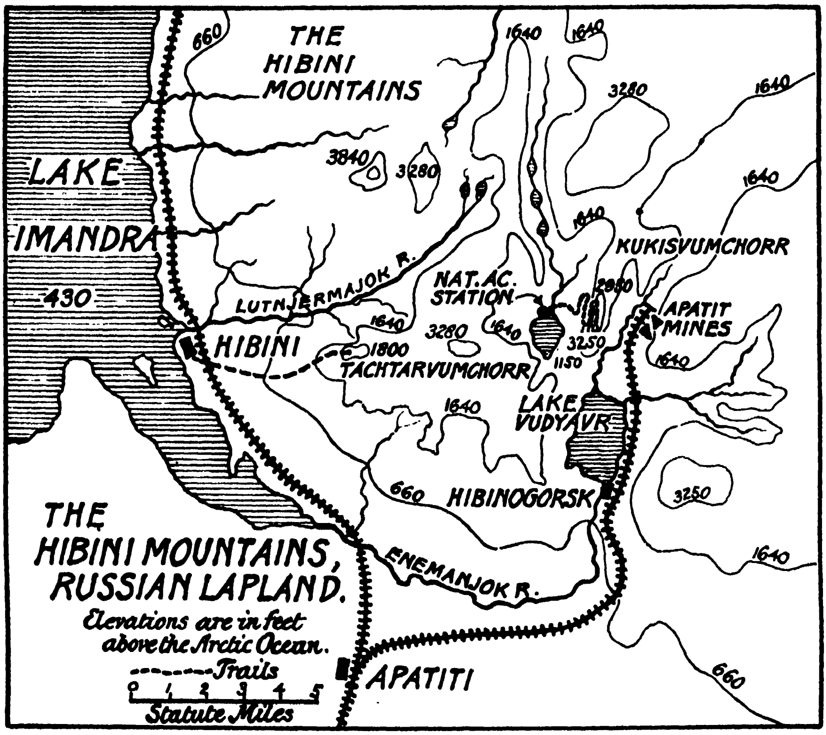

FIG. 2. Map of the Hibini Mountain region of Russian Lapland.

imir Fridoline of the Leningrad National Academy, specialist in entomological biology. To these gentlemen are my thanks due for their courteous assistance. I am also indebted to Mr. W. R. Williams of the New York Botanical Gardens for identifying the mosses, to the late Professor C. C. Plitt of the University of Maryland, for the identification of the lichens, and to Miss Emily Rock for listing and arranging the plants names.

Lake Imandra is 430 feet above sea level (fig. 2). Its shores, where recent foresting has left them untouched, are covered with pine, spruce, and birch. The pine, *Pinus silvestris* var. *fennica*, usually predominates. The spruce is chiefly the Siberian species, *Picea obovata*, with *P. excelsa* also present, and, according to some authorities, equally abundant. There is difficulty

in distinguishing the two. *Juniperus communis* occurs near the lake shore but is more frequent at higher altitudes. Its maximum height is rarely above five feet.

Birches, as bush and prostrate forms, are abundant, especially at higher altitudes, but the lowland tree forms are not numerous. Among the latter are *Betula pubescens, B. odorata* (*B. pubescens* var. *odorata*) and *B. verrucosa*, of infrequent occurrence. *B. kusmischeffii* occurs higher up as a tree-shrub. It and *B. odorata* are hybrids. Two other birches of the Kola Peninsula are *B. tortuosa* and *B. nana*, both typical of higher altitudes.

Alnus borealis and *Populus tremula* occur as scattered specimens, the latter being usually found as a small tree at higher altitudes. *Sorbus aucuparia* forms low bushes in moderate quantity. Neither *Populus tremula* nor *Sorbus aucuparia* characterize the arctic vegetation as strikingly as they do the mountain flora of the southern Soviet Provinces. The willows are abundant, but only in low forms being more typical of the higher slopes where they exist as prostrate plants. Among the nine or more species which are said to occur, *Salix glauca* is most abundant as a tree-shrub along the lake shore. With it occurs *S. lapponica*.

Kreps and Regel distinguish several types of forest associations at the lake shore, with pine and spruce as the dominant members. Pine is the more abundant and spruce exhibits greater variety in its associates. Regel enumerates ten spruce associations distinguished by their undergrowth among which are Picetum myrtillosum, Picetum sphagnosum, and Picetum microbetulosa-empetrosum (fig. 4). Regel mentions five pine associations but Kreps reduces these to three: Pinetum sphagnosum, with *Rubus chamaemorus*, on wet ground; Pinetum hylocosum, with Hypnaceae, chiefly *Hylocomium proliferum* and *Hypnum*, and *Vaccinium*, on moist ground; and Pinetum cladoniosum, consisting of pine and numerous lichens chiefly *Cladonia alpestris*, on dry ground. The spruce gets into all three of these associations and may replace the pine, thus forming the similar associations of Picetum sphagnosum, etc.

The struggle between pine and spruce in the arctic is similar to that in the Caucasus.[2] Pine predominates on dry, sandy, and rocky soil, and spruce on wet sand, but better on clay. There is little pure clay soil in this region and therefore few pure stands of spruce. The clay with its spruce is mixed more or less abundantly with the sand and its pine. Few if any areas exist which have not been repeatedly fire swept. In a fire, the spruce dies first because its large lower branches often sweep the ground and take root while the pine, with its high branches, more easily survives. The temperature factor is also in favor of the pine for spruce seedlings freeze unless well protected by a covering of larger growth, consequently, the pines come in first on

[2] **Seifriz, W.** 1932. Sketches of the vegetation of some southern provinces of Soviet Russia. III. Plant life in the Bakuriani Basin, Minor Caucasus. *Jour. Ecology* **20**: 53–68.

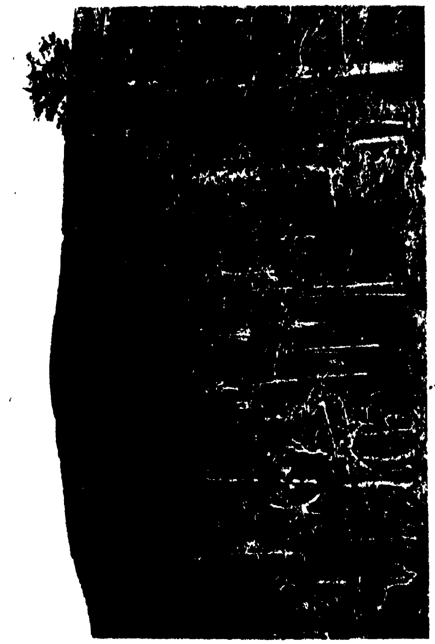

FIG. 3. The lower Hibini Mountains.

FIG. 4. The forest floor of an island in Lake Imandra.

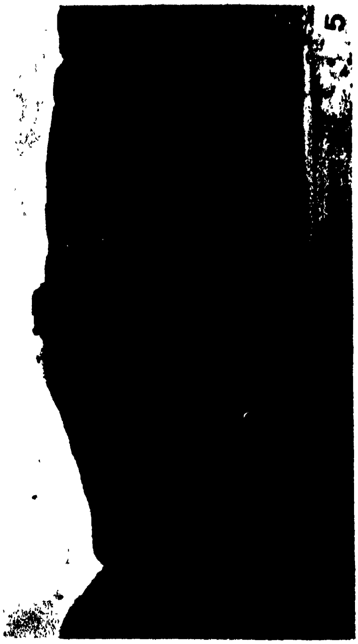

FIG. 5. Small Lake Vudyavr in the Hibinogorsk Mountains.

FIG. 6. The island of Kildin in the Arctic Ocean off the Marman coast.

new, fire-swept soil, and the spruce seedlings follow. The roots of the pine go deep while those of the spruce are superficial, which gives the pine the advantage, particularly on stony ground where it predominates. The spruce holds better in clay soil. Fortunately the spruce is not wholly outdone by the pine; it has one substantial evolutionary factor in its favor, that of vigor, so that in time the spruce should and occasionally does win out over the pine, unless other factors interfere.

A small island in Lake Imandra just off the Hibini Station (fig. 4) is a rich collecting ground, although not a pure association. It presents a typical spruce-pine-moss-Ericaceae complex of the following composition: *Picea excelsa* (*P. obovata*), *Pinus silvestris* var. *fennica, Betula pubescens, B. nana, Salix glauca, S. lapponica, Vaccinium vitis-idaea, V. uliginosum, V. myrtillus, Ledum palustre, Empetrum nigrum, Calluna vulgaris, Rubus chamaemorus, Cornus suecica, Equisetum* spp., *Lycopodium clavatum, Nephroma arcticum, Sphagnum* spp., *Hylocomium proliferum, Hypnum* spp., *Polytrichum juniperinum, Ceratodon purpureus, Bryum caespiticium, Cladonia alpestris,* and *C. rangiferina.*

In such an association complex occur many other plants, scattered or in restricted areas where the ground is more open and drier or moister, but as these plants are typical of other regions none need be enumerated here, except the gem of all the arctic flowers, *Linnaea borealis,* which has a very wide distribution preferring, however, the wooded moors.

The herbarium at Hibini records *Cladonia alpestris* and *C. rangiferina* as the predominating terrestrial lichens. My own collections contained the following additional species for the lowlands at Hibini: *Cladonia coccifera stemmatina, C. deformis gonecha, C. uncialis, Stereocaulon paschale, Nephroma arcticum, Parmelia centrifuga,* and *Cetraria islandica.*

Within the needle forests, or bordering them, are wet moors, bogs, swamps, and open water, each of which harbors a typical vegetation, though there is much intermingling. To distinguish sharply between moor, bog, swamp and tundra is impossible in the present state of confusion of these terms. Moor might better be retained for the dry heaths, yet wet moors, which are not uncommon, as in the North German *Heide,* practically become bogs. Kreps translates the Russian word for "bog" into the German word "moor." Tundra is just as loosely used. The consensus of Russian opinion is that it should be retained for the high (mountain) moors yet it is a convenient term for the low northern moors which duplicate the high moors of the mountains. The wet moors or bogs of Hibini are usually association complexes, but Krebs tells of pure stands of *Molinia caerulea* forming one of the typical sedge moors of the Peninsula. More common are the sphagnum moors with scattered pines. These are ideal habitats for a number of plants which find their home here without characterizing the association. The first half dozen plants of the following list are typical of the moor; the rest are frequent inhabitants

of it: *Sphagnum acutifolium, Molinia caerulea, Carex gracilis, Betula nana, Empetrum nigrum, Ledum palustre, Cladonia* spp., *Marchantia polymorpha, Equisetum palustre, Lycopodium selago, Eriophorum alpinum, Orchis maculata, Drosera rotundifolia, Rubus chamaemorus, Loiseleuria procumbens, Pirola rotundifolia, Phyllodoce taxifolia, Arctostaphylos uva-ursi, Arctous alpina,* and *Pinguicula vulgaris.*

Where the moor becomes swamp or the lake forms inland pools, the following aquatic and semi-aquatic plants occur: *Potamogeton* spp., *Phragmites communis, Carex aquatilis,* and *Menyanthes trifoliata.*

The borders of the moors, the lake shore, and the larger semi-moist burned-over areas, all harbor a considerable variety of plants which cannot be ascribed to any one association, being widely scattered. The more abundant of the flowering species add color to the otherwise somber tone of the arctic flora. The most prolific of these is *Epilobium angustifolium* which in great profusion covers the burned areas from Leningrad to the Arctic Ocean. Among these widely scattered plants are:

Stereocaulon denudatum
Peltigera spp.
Ochrolechia tartarea
Cetraria nivalis
Alectoria ochroleuca
A. divergens
Sphagnum lindbergii
S. fuscum
S. medium
S. balticum (20 spp. occur)
Mnium cincidioides
Nephrodium dryopteris
Equisetum silvaticum
Deschampsia spp.
Carex rotundata
C. alpina (20 spp. occur)
Luzula multiflora
Maianthemum bifolium
Orchis lanceolata
Alnus (*incana*)
Stellaria holostea
Lychnis flos-cuculi
L. alpina
L. viscaria
Viscaria alpina
Trollius europaeus
Ranunculus spp.
Drosera anglica
Rubus saxatilis
Rosa acicularis
Alchemilla sp.
Comarum palustre
Geum rivale
Trifolium repens
Astragalus alpinus
Geranium sylvaticum
Viola canina
V. biflora
V. tricolor
Angelica archangelica (*A. sylvestris*)
Pirola secunda
P. media
Trientalis europaea
Myosotis sp.
Veronica sp.
Bartschia alpina
Euphrasia minima
Rhinanthus sp.
Linnaea borealis
Campanula rotundifolia
Solidago virga-aurea
Antennaria dioica
Achillea millefolium
Tussilago farfara
Matricaria inodora
Cirsium heterophyllum
Saussurea alpina
Taraxacum ceratophorum
T. lapponicum
Hieracium silvaticum
H. alpinum

The sand deltas of the Lutnjermajok River, where the latter flows into Lake Imandra near Hibini, illustrate one of the most interesting of the ecological features of the region. The majority of the species which form the sparse vegetation on the river delta are typical high altitude plants which do not normally occur on the lowlands except where, as here, they have been brought down with the sand. The deltas are formed of nepheline sand (nephelin-syenite) which is brought down from the high regions by the river waters. The most abundant and conspicuous plants in this rather meager delta flora are the typically alpine forms *Saxifraga aizoides* and *Silene acaulis.* They actually thrive better at the lake level than in their natural habitat at a higher elevation. Their presence and healthy condition on the lake shore indicate that altitude, with its characteristic qualities of temperature and light, is after all not always an important factor. Rather does competition determine the successful growth of these plants. At the lower altitude there are no competitors on the deltas, yet the high altitude forms find there the same soil that they would have near the mountain tops. *Silene* occurs in two varieties, one with yellow and one with orange flowers; both may form mounds 18 inches in diameter. There also occur *Silene alpina, Oxytropis sordida, Papaver radicatum* var. *lapponicum, Oxyria digyna,* the rare alpine *Sagina linnaea,* and the thoroughly alpine *Carex rigida,* all high altitude forms transported with their soil to the lowlands. *Poa alpina* may be added to the list although it is a relatively widely scattered grass. Kreps was among the first to call attention to this interesting ecological oddity.

An altitude of 1800 and 2500 feet can be conveniently reached near Hibini in a two or three hour walk from the lake. It is desirable to climb the lower Hibini Mountains near the lake, even though they present a bleak appearance (fig. 3) because the more picturesque Hibinogorsk Mountains (fig. 5) lack the lower altitude plants. Three lichens were collected on the 1800 foot summit of one of the Hibini (Tachtarvumchorr) Mountains which were not seen elsewhere; they are *Cetraria tenuifolia, Gyrophora proboscidea,* and *Cladonia sylvatica.* The following is an account of the altitudinal distribution of plants on both the Tachtarvumchorr and the Kukisvumchorr Mountains.

Hibinogorsk is the new city on Lake Vudyavr, three miles from the recently discovered phosphorus mines. The settlement may be reached by train from Apatiti, or by a twenty hour walk through the mountains from Hibini. The house of the Leningrad National Academy on Small Lake Vudyavr (fig. 5) 1200 feet altitude, serves as a base for the visiting naturalist. At the lake, moors predominate, moors which more closely approach tundra than do the bogs of the lowland. With *Ledum palustre* in abundance, the association is definitely moor and not tundra. A few plants not so far found, were gathered here: *Gymnadenia conopsea, Dianthus superbus, Saxifraga stellaris, Cassiope hypnoides,* and *Gnaphalium supinum.*

Where forest creeps up into the almost treeless Vudyavr Valley, the spruce

is the sole representative of the larger arborescent forms. Pines are few and exist only as dwarf specimens seldom exceeding three feet in height as compared with the large trees found at Hibini.

The treeline on the Kukisvumchorr Mountains is formed by *Picea obovata,* in upright form, and *Betula pubescens.* With these occur *Betula kusmischeffii,* a controversial species of birch which may be a variety, if not merely a synonym, of *B. tortuosa.* The birches here, as throughout Russia, are taxonomically indefinite. If we are to distinguish them *B. kusmischeffii* is the tree-shrub form while *B. tortuosa* is prostrate, much resembling *B. nana* but with larger leaves, ½ inch in length as compared with the *B. nana* leaves which are less than ¼ inch. *B. nana,* a small prostrate shrub, is the most widely distributed species, growing at all altitudes.

The willows offer an even more difficult problem. Ten species occur in the Hibini Mountains: *Salix glauca, S. lapponica, S. phylicifolia, S. reticulata, S. herbacea, S. rotundifolia, S. polaris, S. alpina* (*S. polaris*), *S. myrsinites,* and *S. lanata.* None form large trees. *S. lanata* is a bush form, growing abundantly at the tree line. *S. reticulata* and *S. herbacea* are small and prostrate, the latter becoming more abundant higher up.

Sorbus aucuparia is not infrequently met with. *Populus tremula* is rare and seldom attains a height of more than 18 inches. It is found mostly on southern slopes.

At the tree line a number of plants find their upper limit and others make their first appearance, while still others take on ecological modifications. This last is true of the spruce which at higher altitudes is prostrate in form. Another prostrate gymnosperm is the juniper which could have been mentioned among the lowland plants, where it is moderately abundant and grows to a maximum height of 6 feet. Here, at 1700 feet, it lies closer to the ground and most authorities refer to this prostrate arctic juniper as *J. nana.*

Linnaea borealis finds its upper limit near the tree-line. This is also true of *Dianthus superbus.* A plant typical of the willow scrub at this altitude is the small (15 inch) *Rubus saxatilis* which here replaces the related *R. chamaemorus* of the lowland. Another and quite rare tree line plant growing always in isolated wet rocky exposures on southern slopes, is *Cotoneaster siberica.* With it occur a *Rosa, Rubus saxatilis,* and the two grasses, *Melica nutans* and *Molinia caerulea.*

While ferns grow in the lowlands, it is in the wet ravines and gorges above the lake shore that they are most abundant. They climb to near the tree line, but are never profuse. The species collected were *Phegopteris dryopteris, Dryopteris linneana,* and *Aspidium lonchitis.* This modest list indicates the paucity of ferns in the Hibini Mountains, but it does not convey quite a fair impression, as other species have been reported, namely, *Woodsia alpina, Cystopteris fragilis, C. montana, Polystichum lonchitis, Athyrium felix-femina, A. alpestre, Allososus crispus,* and *Polypodium vulgare. Botrychium simplex* was also found, the only species listed for the Hibini Mountains.

But one moss, *Dicranoweisia crispula*, was collected at Hibinogorsk.

Five hundred feet above the tree line, at an altitude of 2200 feet, there grows a true subalpine flora (pseudo-tundra) intermixed with species from below and above. All plants collected in this subalpine zone between 1800 and 2500 feet, i.e., at an average altitude of 2200 feet, are given in the following three lists, the first of which includes the plants typical of lower altitudes, the second, the plants which characterize the subalpine zone, and the third, the plants typical of the higher alpine flora. Such widespread forms as *Betula nana* and the Vacciniums are classified with difficulty; they characterize the lowland swamps as much as they do the subalpine slopes.

Typical of Forest (below 1300 feet)	Subalpine (1800–2500 feet)	Alpine (above 2500 feet)
Hylocomium proliferum	*Juniperus* spp.	*Rhacomitrium hypnoides*
Lycopodium aurantia	*Tofieldia alpina*	*Salix herbacea* (*S. alpina*)
Juncus spp.	*T. borealis*	*Silene acaulis*
Polygonum viviparum	*Coeloglossum viride*	*Saxifraga aizoides*
Alchemilla sp.	*Salix reticulata*	*S. oppositifolia*
Geranium sp.	*S. myrsinites*	*Dryas octopetala*
Pirola minor	*S. phylicifolia*	*Cassiope hypnoides*
P. uniflora	*Betula nana*	*Veronica alpina*
Loiseleuria procumbens	*B. kusmischeffii*	*Pedicularis lapponica*
Andromeda polyfolia	*Oxyria digyna*	
Calluna vulgaris	*Ranunculus glacialis*	
Pinguicula alpina	*Papaver radicatum*	
Campanula	*Sibbaldia procumbens*	
Solidago	*Potentilla alpestris*	
Antennaria dioica	*Oxytropis sordida*	
Saussurea alpina	*Viola montana*	
	Diapensia lapponica	
	Phyllodoce caerulea	
	Cassiope tetragona	
	Vaccinium vitis idaea	
	V. uliginosum	
	V. myrtillus	

Among the above plants a number make their first appearance at this altitude (2500 ft.), these are *Veronica alpina*, *Pedicularis lapponica*, and the two *Cassiope* species. Both of the last mentioned prostrate Ericaceae are distinctly high altitude forms, the smaller of which, *Cassiope hypnoides*, climbs the higher. *C. tetragona* is a rare plant, the mountains at Hibinogorsk being among its few habitats. The willows are especially interesting because of their small size and ecological change in form, thus *S. myrsinites* occurs at lower altitudes where it attains a maximum height of 3 feet, but here in the subalpine belt it becomes a low plant with very small leaves, the old ones of which persist through the second summer. The smallest of the willows, which lies very close to the ground like a creeping vine, is *S. herbacea* (*S. alpina*). *S. reticulata* also is prostrate here, but has larger leaves. *Betula nana* is as abundant at 2200 feet as it is in the bogs below at 430 feet. This small-leaved prostrate birch therefore extends from the lowlands up to the edge of the high alpine tundra.

The preceding list of plants growing in their natural habitat at 2500 feet

contains the names of those specimens found growing on the Lutnjermajok River delta, at Hibini, including *Saxifraga aizoides* and *Silene acaulis,* which grow equally well at both altitudes.

No marked altitudinal distribution of lichens was observed, although lichens (and mosses) may show as striking an altitudinal distribution as do flowering plants. Those collected on the Kukisvumchorr Mountains at Hibinogorsk are: *Stereocaulon alpinum, Cetraria islandica, Solorina crocea, Gyrophora proboscidea,* and *Rhizocarpon geographicum astrovirens.*

The summit of the ridge, at 3250 feet, is a rocky alpine tundra. The soil is badly weathered and the vegetation sparse. Climbing still higher along the ridge, one reaches the maximum altitude of the mountain, 3400 feet. The following plants were observed at the top: *Cladonia* (and other lichens), *Dicranum* spp., *Polytrichum* spp., *Lycopodium alpinum, Deschampsia* sp., *Carex* spp., *Juncus* spp., *Salix alpina* (*S. herbacea*), *Silene acaulis, Saxifraga aizoides, Dryas octopetala, Empetrum nigrum, Loiseleuria* sp., *Phyllodoce caerulea, Vaccinium vitis-idaea, V. uliginosum, Cassiope hypnoides, Bartschia* sp., *Campanula rotundifolia,* and *Solidago virgaurea.*

Dryas octopetala is credited with being the flowering plant which climbs highest; *Silene acaulis* and *Saxifraga aizoides* are close behind.

The journey north to the Arctic Ocean and the Island of Kildin was made in order to follow the change in type of vegetation with change in latitude. If the successive altitudinal zones through which one passes in climbing the Hibini Mountains were brought down to sea level and placed one after the other as one travels north, a fairly accurate picture of the arctic lowland flora extending from Hibini to the Arctic Ocean, a distance of 125 miles, would be had. Only two features of this northernmost vegetation of western Russia will be added to that already given, namely, a delineation of the tree line, and a description of the flora of the Island of Kildin.

The tree line on the Kola Peninsula has been established by Kreps. It is better given by a line on the map (fig. 1) rather than in words. It represents the northern limit of the needle forest. Deciduous trees (birch, willow, and poplar) get down to the ocean shore along all river banks. The northern limit of the needle forest does not run parallel to the coast nor to the lines of latitude, but approaches parallelism with the ice barrier. This is due to the Gulf Stream, which, north of Norway (between latitude 73° and 75° N.), divides into four branches. The southern one sweeps the coast of the Kola Peninsula until it disappears at longitude 40° E. Here the ice barrier commences, closing the White Sea in winter but leaving the north Murman coast open the year round. Alexandrovsk (its name was recently changed to Polarnoje) is the only Russian seaport which is never closed to shipping because of freezing.

One-half mile off the Murman coast, 25 miles from Alexandrovsk, is Kildin (fig. 6). It is a treeless island, one and a half to two miles across and three or four times this in length. It rises to a maximum height of about

1000 feet. Its shore is precipitous and its surface a relatively flat plateau which is almost pure and typical tundra, if we may use this convenient term for arctic moors. Here and there on the island are wet depressions which harbor a bog vegetation. One small lake exists. It is separated from the sea by a narrow, rocky, natural causeway. This lake is one of the few, if not the only one, of its kind. Its surface is fresh water to a depth of several inches supplied by surface water from the island, while its deeper water is salty. The lake was probably cut off from the ocean in early times leaving a subterranean connection with the sea. Its surface water is sufficiently fresh to permit drinking, and its deeper water contains marine organisms of great variety, such as codfish and echinoderms.

Were the alpine, and part of the subalpine, flora of the mountains at Hibinogorsk taken from their heights at 2500 to 3200 feet, and transferred to the plateau of Kildin, we should have a very close reproduction of the tundra existing there. Some twenty species not yet named were collected on Kildin. One of the most interesting of these is *Saxifraga rosea.* Among the others are: *Calamagrostis neglecta, Cerastium sylvaticum, Caltha palustris, Sedum roseum, Parnassia palustris, Filipendula ulmaria, Angelica archangelica* and *Andromeda polifolia.*

The following list contains all plants collected on Kildin, 270 miles north of the Arctic Circle, in latitude 69° 5′. About two hundred species have here been named to characterize the flora of the Hibini region and Kildin. The total number of species ascribed to Russian Lapland is approximately four hundred and fifty.

Stereocaulon alpinum
Haematomma ventosum
Rhizocarpon geographicum
R. geographicum atrovirens
Lecidea confluens
Gyrophora polyphylla
Nephroma arcticum
Rhacomitrium hypnoides
Mnium cincidioides
Aulacomnium turgidum
Drepanocladus exannulatus
Dryopteris sp.
Equisetum sp.
Lycopodium annotinum
L. alpinum
Juniperus communis
J. nana
Calamagrostis neglecta
Eriophorum polystachion
E. vaginatum
Carex tetragona
C. hypnoides
C. rotundata
Juncus polyformis
Orchis maculata
Salix lanata
Betula nana
Rumex acetosella
Polygonum viviparum
Sagina linnaea
Cerastium sylvaticum
Dianthus superbus
Ranunculus pygmaeus
Caltha palustris
Sedum roseum
Saxifraga rosea
Parnassia palustris
Rubus chamaemorus
Alchemilla sp.
Dryas octopetala
Filipendula ulmaria
Comarum palustre
Geum rivale
Oxytropis sordida
Geranium pratense
Vicia cracca

Empetrum nigrum
Epilobium palustre
Angelica archangelica
Diapensia lapponica
Cornus suecica
Pirola secunda
P. rotundifolia
Loiseleuria procumbens
Arctous alpina
Vaccinium vitis-idaea
V. myrtillus
V. uliginosum
Andromeda polifolia
Trientalis europaea
Bartschia alpina
Euphrasia officinalis
Pedicularis sceptrum
Melampyrum pratense
Rhinanthus minor
Pinguicula palustris
Linnaea borealis
Campanula rotundifolia
Solidago virgaurea
Antennaria alpina (*A. dioica*)
Achillea millefolium
Saussurea alpina
Cirsium heterophyllum
Hieracium sp.

REVIEWS

The Structure and Classification of Peat Deposits in the United States [1]

This is a comprehensive and authentic account by the foremost student of the subject in America. It is dynamic in character, since the distinctions are chiefly derived from succession in terms of the climax and climate concerned. As is well known, no other course of development records itself with anything like comparable detail and completeness, to permit an intimate correlation between succession and structure. Thus, the resulting profile consists not merely of a unique series of fossil communities, but it also carries the impress of physiographic and climatic changes.

The author follows Weber in the major division of peat deposits into *oligotrophic* and *eutrophic*, but broadens the definition to include the effect of climate as a major feature, while the intermediate group is termed *mesotrophic*. The main subdivision is based essentially upon the climaxes concerned and a further differentiation is made in accordance with edaphic conditions and the sequence of the stages leading to maturity. The final groupings rest upon the degree of decomposition of the parent materials, and within this upon the characteristics of the profiles themselves. For example, the Oligotrophic group comprises the Laurentian and Columbian subgroups, and the former contains two series, Algonquin and Champlain. The Algonquin series is represented by two major types in terms of materials, namely, woody-fibrous-moss peat and fibrous-moss peat, each of which is further divided into four regional types. The Mesotrophic group is constituted by the Inland and Coastal subgroups, the first with three and the second with one series, while the Eutrophic group comprises the Everglades, San Joaquin, and Puget Sound series.

To the ecologist interested in the dynamics of vegetation, the discussion of each regional type will afford a wealth of concise information. This relates to the general character of the deposit, to the structure and seral features of the existing vegetation, and to the developmental morphology of the profile. The latter exhibits five community horizons in the woody-fibrous-moss peat of the Oneida type, viz. sedge-reed at the base, followed successively by woody, sphagnum, woody, and sphagnum moss peat, while for the Northome type in Minnesota the sequence is sedimentary, sedge-reed, woody, and sphagnum peat. The layers in the fibrous-moss type are essen-

[1] **Dachnowski-Stokes, A. P.** Peat deposits in United States of America: their characteristic profiles and classification. *Handbuch der Moorkunde* 7: 1–140; 23 *figs.*, 9 *pls.* Borntraeger, Berlin. 1933.

tially similar, but with the omission of a tree stage. The mesotrophic deposits lack the sphagnum layer, may or may not display a woody section, and often possess a marl layer at base. Eutrophic profiles are typically simpler, consisting chiefly of typical reed-swamp dominants, *Cladium* in the Everglades and *Scirpus-Typha* on the Pacific Coast, with a sedimentary layer not infrequent and a woody one exceptional.

The excellent text-figures and half-tones serve to illuminate as well as illustrate the text, and those of the profiles are particularly valuable in definitizing the various types.

FREDERIC E. CLEMENTS

CARNEGIE INSTITUTION OF WASHINGTON,
SANTA BARBARA, CALIFORNIA

THE CHEMISTRY OF FRESH WATERS

From an ecological standpoint, the various substances held in solution by natural waters constitute one of the most important elements in the environment of aquatic organisms. This is true especially of the solutes which are essential for the growth of the phytoplankton and the large aquatic plants. A knowledge of the scarcity or abundance of these dissolved materials gives a clue to the fertility of the aquatic soil and such information can be obtained only by chemical analyses. The recent volume by Maucha[1] gives a detailed account of the various methods and the apparatus used in making such analyses. Most of the methods which he presents were devised by Winkler, but modifications are included in some of the procedures. Directions are given for quantitative determinations of the dissolved gases as well as of the different mineral constituents found in fresh waters. Theoretical discussions of both methods and results are also given. The volume is a worthy companion of the previous ones dealing with inland waters which have been issued under the editorship of Dr. Thienemann.

The brochure prepared by Pia[2] deals with the carbon dioxide and calcium content of natural waters. It contains an extended discussion of the forms in which the carbon dioxide exists in fresh water and also a consideration of the solubility of calcium carbonate at different temperatures and under different carbon dioxide pressures. The latter part of the volume treats of the deposition of calcium carbonate, of the forms in which it is deposited and of the various agents which cause its deposition. Plants play an important role in the deposition, such as green and blue-green algae, diatoms and the large aquatic plants; mollusks are the most important decalcifying agents among the animal forms.

C. JUDAY

UNIVERSITY OF WISCONSIN,
MADISON, WISCONSIN

[1] **Maucha, Rezsö.** 1932. Hydrochemische Methoden in der Limnologie. *Bd. XII, Thienemann's Die Binnengewässer.* x + 173 pp., 36 figs. *Stuttgart.*

[2] **Pia, Julius.** 1933. Kohlensäure und Kalk: Einführung in das Verständnis ihres Verhaltens in den Binnengewässern. *Bd. XIII, Thienemann's Die Binnengewässer.* vii + 183 pp. 17 figs. *Stuttgart.*

Game Management[1]

Professor Leopold's "Game Management" maintains game range can be altered to give greater productivity, that game can be restored by the creative use of the same tools which have destroyed it, as the plow, cow, fire and gun. The "factors" and "influences" that determine abundance in all species, rather than information for particular species or areas, are the concern of and provide the topic headings for the book. (Upland game birds however supply the great majority of the examples used in the discussion.) The author undertakes something new in his attempt to adapt the art of game management to biological principles and American game species, conditions and traditions.

The text comprises 18 chapters of which the first 5 deal with the theory of game management. Included in these is one chapter dealing with its history and purposes, and one on its mechanism, as productivity, differences in breeding potentials and limiting factors. Next in order are two chapters on properties of game populations, their fluctuations, types of population curves, tolerances, sex and flock habits. Chapter 5 considers game range, environmental types, interspersion of types and a classification of game species with respect to their range requirements. The second major division consists of 10 chapters dealing with management technique. The first chapter here is devoted to game census. Then follows a discussion of management and "diagnosis" of productivity, "diagnosis" meaning weighing the "factors" (forces reducing the numbers or retarding the increase rate), and selecting one or more for control. Chapters 8–14 deal with the manner in which the "factors" operate and the actual execution of the control measures including discussions of game refuges, accidents (mortality from physical causes), and the control of hunting, predators, food and water, cover and disease. A chapter on miscellaneous techniques which treats artificial propagation, nesting studies, maps and surveys, concludes part two. The final three chapters, under the heading of game administration gives the author's viewpoint on reasons for perpetuating a game supply, incentives for securing widespread practice of management, and game management as a profession.

The book is replete with graphs and charts (19), maps (14), and tables (55), containing an enormous amount of data and so arranged that it aids greatly in presentation of the subject. It is well indexed, has a glossary of terms used in game management and a bibliography of 428 titles. A very attractive feature of the work are the drawings by Allan Brooks, two of these are full page illustrations.

Students of game will welcome this book as a starting point in a sounder and better understanding of American game problems, and the formulation of constructive programs of land usage for game production. To the biologist, forester and agricultural expert it offers an explanation of how his own

[1] **Leopold, Aldo.** 1933. Game Management. xxi + 481 pp., 2 plates, 55 tables, 35 text figures. *New York, Charles Scribner's Sons.* $5.00.

science and practices are related to the field of wild-life management. To all who are interested in the animal life they observe while afield it presents an instructive and very well written interpretation of changes and relationships that are an integral part of wild animal populations.

D. IRVIN RASMUSSEN

U. S. FOREST SERVICE,
OGDEN, UTAH

FAUNA OF THE NATIONAL PARKS OF THE UNITED STATES[1]

" Fauna of the National Parks " is a report of a preliminary survey of the vertebrate faunal relationships of the parks with emphasis on the influences man has exerted on the natural conditions. It has as its objective, the presentation of, " a report which would delineate the existing status of wild-life in the parks, analyze unsatisfactory conditions, and outline a proposed plan for the orderly development of wild-life management."

The analysis of the major types of wild-life problems (pp. 19–84), contains a discussion of the wide range of maladjustments that the survey revealed in the park system. The problems encountered are attributed to be of historical (earlier influences), geographical (failure of parks as independent biotic units) or competitive (conflict between man and animals) origin. Some of the varied and interesting examples that are analyzed are; question of re-establishing mountain sheep in Yosemite, lack of winter range for elk in Rocky Mountain, special protection for the few remaining trumpeter swans in Yellowstone, a place for the wolverine in the United States, caribou and reindeer hybridization danger in Mount McKinley, oversupply of deer in the floor of Yosemite, and property damage of the too numerous bears in several parks.

In a conspectus of the wild-life problems of each park (pp. 85–146) the larger vertebrate species are considered in relation to the ecology of the parks in which they occur. The almost universal need for boundary adjustments to coincide with natural barriers and to include complete biotic units within the various parks, especially the need for additional winter range for the larger ungulates, appears as the most common deficiency of the national parks.

The final short but perhaps most interesting section to many ecologists is the suggested national park policy for the vertebrates (pp. 147–148). This contains twenty brief statements of policies relative to areas, boundaries, management, relations between animals, and visitors and faunal investigations. They represent the authors' conclusions, based on a careful survey, of methods by which accurate samples of primitive America might be preserved for ob-

[1] **Wright, George M., Joseph S. Dixon, and Ben H. Thompson.** 1933. Fauna of the National Parks of the United States. A Preliminary Survey of Faunal Relations in National Parks. iv + 157 pp., 56 figs. *Washington, United States Government Printing Office.* Obtainable from Superintendent of Documents, Washington, D. C. $0.20.

servation of the recreation seeking public and scientists, at the present time and for the future.

D. Irvin Rasmussen

U. S. Forest Service,
Ogden, Utah

Handbook of Frogs and Toads [1]

All who are interested in the study of nature will welcome this valuable handbook which appears as Volume I of a projected series of Handbooks of American Natural History. "The plates and script are meant to cultivate an interest in the lay mind and help the beginner in his or her quests." Most of the species of frogs and toads of the United States and Canada are treated according to a topical outline which includes names, range, habitat, size, general appearance, structure, voice and breeding supplemented by notes recorded by the authors or by other workers in the field. With few exceptions photographs from life are reproduced, many appearing for the first time and so filling a long felt need. By virtue of numerous line drawings illustrating the characters utilized, the key included in the general discussion is rendered understandable even to the amateur naturalist. The bibliography, arranged for the most part according to states and provinces, is well selected. The book is full of information which will prove of great value to zoologists as well as to classes in nature study and lovers of outdoors in general. It should be available in every school library.

B. B. Brandt

Duke University

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[1] **Wright, Anna Allen, and Albert Hazen Wright.** 1933. Handbook of Frogs and Toads. ix + 231. *Ithaca, N. Y., Comstock.* $2.50.

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NOTES AND COMMENT

The Depth Distribution of Some Aquatic Plants

While making quantitative studies of the plankton and of the bottom fauna of Wisconsin lakes, some interesting depth records have been obtained for a few aquatic plants. The first observation of this character was made on Green Lake in August, 1921. The mud samples obtained from a certain area of this lake were covered with a thin felt-like, white or grayish growth of *Oscillatoria prolifica.* The filaments of this alga were compacted into a mat about 2 mm. thick which could be readily removed from the surface of the mud in rather large pieces. A general survey showed that this mat covered an area of about one square kilometer of the lake bottom where the water was 65 to 68 meters deep. This was far below the zone of photosynthesis as the solar energy was reduced to about one per cent of the amount delivered to the surface at a depth of 8 meters. The lack of solar energy and the white or grayish appearance of the mat suggest that this bottom growth of *Oscillatoria* was taking place saprophytically. Also the temperature of the bottom water in this region was only 5.4° C.

A large growth of *Oscillatoria* was found in the 10–15 meter stratum of water in Trout Lake for a period of about a month, beginning in late July, both in 1932 and 1933. Experiments with cultures of green algae at that time showed that the compensation point fell somewhere between 10 and 15 meters in both summers. Observations also showed that one per cent of the solar energy delivered to the surface of the lake penetrated to a depth of about 9 meters and that it declined to 0.05 per cent at a depth of 15 meters.

Some bottom dredge hauls made at a depth of 20 to 25 meters in Black Oak Lake in August 1928 yielded several large masses of *Aphanocapsa;* these algal colonies ranged from one to two centimeters in maximum diameter and they had a purplish color. The transparency of the water of this lake is such that one per cent of the solar energy reaching the surface penetrates to a depth of about 10 meters. In comparison with the foregoing algal records, Kindle[1] found *Cladophora* and diatoms growing at a depth of in Lake Ontario. *Jour. Ecol.* **3:** 149–152.

Three species of moss, namely *Drepanocladus fluitans submersus, Fontinalis antipyretica* and *Chiloscyphus rivularis,* grow at depths of 18 to 20 meters in Crystal Lake and in the deepest water of Weber Lake, namely 13.5 meters. The first two species have been reported by Williams.[2] The water of Crystal Lake is very soft and transparent; a maximum disc reading of 13.6 meters has been recorded. From one per cent to approximately four per cent of the solar energy at midday penetrates to a depth of 18 meters. The temperature of the 18–20 meter stratum ranges from 8° to 11° C. in summer. The water of Weber Lake is very soft also, but it is not quite so transparent and the bottom temperatures are somewhat higher. One of the interesting characteristics of these mosses is the fact that they contain a rather high percentage of iron. In Crystal Lake 1.2 per cent of the dry weight of these plants consists of Fe_2O_3 and in Weber Lake 1.8 per cent. This percentage is substantially the same as that of the bottom muds on which they grow.

C. Juday

University of Wisconsin

[1] **Kindle, E. M.** 1915. A new bathymetric record for attached algae and diatoms 150 feet (46 meters) in Lake Ontario.

[2] **Williams, R. S.** 1930. Some deep-water mosses. *Bryol.* **33:** 32.

A Rapid Survey Instrument for the Measurement of Light Intensity under Water

Most of the methods for measuring light intensity have been applied in the study of light absorption by water. An excellent bibliography is given by Erikson.[1] Many of these methods are slow or technically difficult and are not well adapted to field survey work.

While working with plants immersed in constant temperature water baths it was necessary to measure the light intensity accurately at the surface of the plant. For this purpose a Weston photronic cell was enclosed in a pyrex glass cell with a polished plane surface and side arm. A top view of this is shown in figure 1B. The side arm is 2 cm. inside diameter at one end to receive the pins of the photronic cell and is drawn down to 8 mm. diameter which is just large enough for the rubber cable to pass through. The heavy rubber-covered wire leads are pulled through the side arm and permanently fastened to the pins of the photronic cell. The photronic cell is then placed in the glass vessel, face against the plane surface. Cotton packing is put in and the bottom closed with a large soft rubber stopper. The side arm is made air tight with a joint of gum rubber tubing and wire bands. The cell withstands one atmosphere pressure easily and, with sufficient cable, measurements can be made to depths of 30–40 feet.

The small pocket-size Weston foot-candle meter has been used as the indicating instrument. For this purpose a double-throw switch and two binding posts were mounted on the side of the bakelite box. When the leads from the water cell are attached a reading can be taken from the photronic cell which comes with the meter or the outside cell, depending upon the way the switch is thrown. The water cell can be standardized in a few minutes under an electric light in a dark room simply by making alternate readings and reversing the switch.

Table I. *Transmission of light through water, expressed as percentage of surface intensity*

Depth in feet	St. Croix River, Oct. 1 Sun up	(4 P.M.)	Sun down		Mississippi, Oct. 21 1 P.M.	Bright sun
1	77	72	52.6	56.3	64	64
2	46	43	31.6	31.3	39	40
3	32	30	21.1	19.0	27	28
4	20	20	12.6	12.5	18	19
5	13	12	5.2	5.2	12	11.7
6	9	9			7.5	7.5
7					4.5	4.5
8					3.0	3.0

Since this small meter only reads to 500 foot-candles it is necessary to cut down the light intensity for outdoor work. A neutral filter for this purpose is easily made from several layers of pure white, thin filter paper under a circular glass. These are dropped on to the glass face of the photronic cell and held in place by a strip of rubber glued to the cell wall. Only a few minutes in the dark room are required for standardizing the filter. We have used these filters for more than a year and find that they remain perfectly constant in light transmission. A filter with a factor of 20X is used for air measurements and 10X for measurements under water.

If only the intensities at greater depths are wanted no filter is needed on the water cell. Without the filter readings to 1 foot-candle are possible.

A copper case (fig. 1A) is used to protect the cell. The heavy pipe screwed into a

[1] **Erikson, H. A.** 1933. Light intensity at different depths in lake water. *Jour. Opt. Soc. Amer.* **23**: 170–177.

nut soldered to the bottom holds the surface of the cell perfectly horizontal. There is a hole in the bottom so that water flows in through the pipe and fills the space between the metal case and the glass cell. This prevents the trapping of air which might tilt the vessel from the horizontal. Fine copper wires lead to a fishing line on which are markers at one-foot intervals.

By throwing the switch, alternate air and water readings are made at each depth.

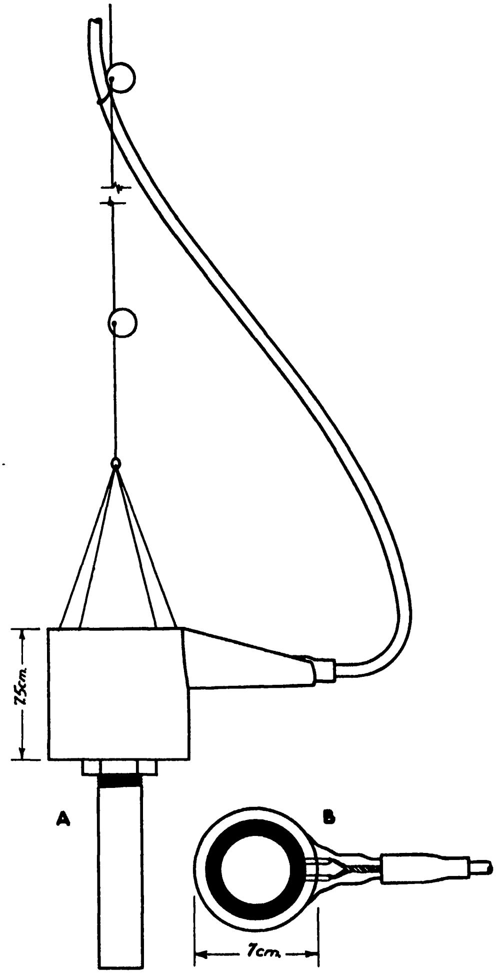

FIG. 1. A. Side view of the apparatus hanging in position for a measurement. The copper case is open at the top and contains the glass covered photronic cell. B. Top view of glass covered photronic cell showing the connection of the pins of the cell to wires of the rubber-covered cable.

After applying the known factors the per cent transmission is readily calculated. Duplicate readings can be made to agree very closely. Table I gives some examples of readings made in the St. Croix and Mississippi Rivers. The former were made from a boat in mid-stream at Prescott, Wisconsin; the latter from the municipal docks, Minneapolis. Duplicate readings are given.

The readings made in the St. Croix are much lower after sun down. It is evident that the time of day makes considerable difference in percentage transmission. Such a series of duplicate readings can be made in a few minutes.

The photronic cell is specific in its response to different wave lengths and this must be kept in mind when interpreting results obtained with it. Fortunately the cell has maximum sensitivity at about 5800 A.U. and very low sensitivity at 7000 A.U. Therefore in shallow water the specific absorption of water has little effect and the fall in intensity must be attributed largely to solutes and suspended matter.

George O. Burr
M. M. Burr

Department of Botany,
University of Minnesota

The Need for Natural Areas

Mr. R. D. Forbes, Director of the Allegheny Forest Experiment Station, writing in *American Forests*, February, 1934, says that "999 acres of forest land out of a thousand in the territory of the Allegheny Forest Experiment Station have been cut over. The thousandth is virgin timber. The thousandth acre will repay careful study." He goes on to point out that on the 999 acres Nature's record has been often hopelessly obscured by the heavy hand of man and by fire.

In the Southwest where so great a proportion of the land is given over to grazing by livestock, biologists find that it is very difficult to find any land at all under natural conditions. In some localities, over-grazed over a vast extent of country, there *is* no thousandth acre. This means that there is no norm with which to compare the vegetation, animal life, and the soil, as they now appear. One may interview old-timers and get from them valuable hints as to the early condition of the country—its soil, streams, grasses, brush, trees, and wild life—but conclusive demonstration is lacking. The existing situation emphasizes in no uncertain terms the need for saving sample tracts in all important types under as nearly as possible original conditions to serve as a guide for present practice. Disturbance of original conditions is inevitable, under the best administrative regulation, but if areas showing natural conditions were available for observation, the administrator and his scientific advisers would be able to determine just how far management could safely go in modifying the original conditions in the process of grazing or other land use.

In a recent inspection of the Gila Valley near Safford, Arizona, with reference to the effects of rodents and rabbits on range conditions, including erosion, it was deemed desirable to locate, if possible, an area under natural conditions so as to determine just how far the land in its present seriously denuded condition had departed from its original state. Although a personal search for relict areas was made, and officials of the Soil Erosion Service and of the Forest Service consulted, we could get no track of any areas under natural conditions. Even the cemeteries, which frequently are fenced in and show something like original conditions, had been carefully cleaned of all natural vegetation. The lack of an area under natural conditions with which to compare the present situation is a very real one and leaves a gap in our information which it is impossible to fill. Our conclusions regarding the feasibility of rodent control, erosion control, fencing, regulation of stock, and other measures for bringing back the land rest to a considerable extent upon our having the complete picture of conditions formerly and at present.

There is increasing need for the preservation of sample areas as large as practicable under natural conditions. These areas should include samples of all the important agricultural range and forest types. In working for the preservation of such areas under natural conditions, the various State organizations, the U. S. Biological Survey, the Forest Service, the National Park Service, and the Ecological Society of America are

performing a service of no small importance to the research men and administrators of the future.

WALTER P. TAYLOR

U. S. BIOLOGICAL SURVEY,
UNIVERSITY OF ARIZONA

NOTES ON THE WATER LETTUCE, *Pistia stratiotes* LINN., AS A NURSERY OF INSECT LIFE

Some aquatic plants are known to have a deleterious effect on certain insects. Others by furnishing sustenance, protection from adverse climatic conditions and predacious enemies, etc., provide conditions that are favorable for their development. In association with the favorable conditions thus provided a few insects have become adapted to pass their immature stages with certain species of these plants most compatible with their existence.

The water lettuce, *Pistia stratiotes* Linn., is one of the plants that seems to be extremely favorable to insect life. This plant consists of a loose rosette of thick, spongy, wedge-shaped leaves. Large specimens of the plant may have from sixteen to twenty leaves, some of which frequently attain a length of more than nine inches. The inner leaves of the rosette may have a nearly vertical position while the older, outer leaves are more horizontal and lie close to the surface of the water. Plants of this species when occurring in tightly packed masses may have many more of the leaves upright than do those that are in loose groups. Although this plant floats on the water it usually rides low enough to bring the base of the rosette just beneath the surface which results in some water being present in the crown of the plant. *Pistia* has a wide distribution, being present in nearly all tropical and sub-tropical regions of the world. The importance of this plant as a nursery of insects that are of concern to man and animals first began to be recognized a number of years ago.

Moore ('10) seems to have first attracted the attention of entomologists to this plant by his discovery of the association of the immature stages of the mosquito, *Mansonia titillans* Walker, with *Pistia.* The eggs of this mosquito are deposited on the under side of the leaves of the plant and the larvae and pupae attach themselves with their air-tubes to the filamentous rootlets. They remain thus attached beneath the surface of the water during their early stages and obtain their supply of oxygen from the tissues of the plant. As an indication of how abundantly *Mansonia* may breed in connection with this plant it may be stated that the writer (Dunn, '18) has reported collecting fifty-one larvae from the roots of one plant.

Zetek ('20) reported *Anopheles* mosquitoes breeding among *Pistia* in the Canal Zone. He states, "Our joint inspection revealed larvae of *Anopheles albimanus* Wied., and *A. tarsimaculatus* Goeldi, to be plentiful among the leaves of the water lettuce."

Important observations have been made by Macfie and Ingram ('23) on the relation of *Pistia* to the breeding of mosquitoes and other biting insects in West Africa. They presented an extensive list of mosquitoes and Ceratopogonine midges that they found associated with this plant. Included in the list were six species of *Anopheles.*

Observations of a similar nature were made by Curry ('32) in discovering that the larvae of *Anopheles bachmanni* are found in the crowns of *Pistia* in the Canal Zone. In reporting on this he states, "Larvae of *A. bachmanni* are frequently encountered in the quiet inlets of Gatun Lake and other bodies of still water, but only within the crowns of water lettuce (*Pistia stratiotes*). Several of us have spent hours in pools where it was plentiful, searching both within and without the crowns of the plants, and not a single larva was found outside the circumference of the plants, where these had not been previously disturbed so as to dislodge the larvae."

A recent paper by Iyengar ('33) describes very interestingly the process by which three species of mosquitoes, *Mansonioides annuliferus, M. uniformis* and *M. indiana,* attach their eggs on the lower side of leaves of *Pistia* in south India.

The association of larvae of Tabanidae with *Pistia* plants seems to have been first observed by King ('26) in North Africa who writes of this as follows: "A few larvae of *Tabanus fasciatus niloticus* were obtained on 4th. March, 1925, near Renk, on the White Nile, their habitat being the Nile cabbage (*Pistia stratiotes* Linn.). They were by no means common, a search of a couple of hours yielding but seven specimens. They were lying submerged in the water, supported on the bases of the lower leaves in such a position that their caudal respiratory siphons could be extended to reach the surface of the water, and never more than a single larva occurred on an individual plant."

Lutz ('28) discovered a second species of Tabanidae, *Lepidoselaga lepidota,* living in the rosette of leaves of a *Pistia* near Maracay, Venezuela, and discusses this as follows: "A principios de octubre de 1925, nuestro sirviente de Laboratorio, encontró en la roseta de una *Pistia stratiotes* (vulgo repollito de agua) sobre la parte superior que siempre se mantiene seca, una larva de tabanido que llamó nuestra atención, . . . No nos parace que la presencia de la larva en la *Pistia* se obra de casualidad. Antes pensamos que sea una adaptación como la que se observa en las larvas de *Mansonia* para la misma planta, pues siendo ésta muy frecuentada por pequenos moluscos acuáticos que viven en la base de las hojas donde ponen sus huevos, la alimentación está de hecho garantizada, tanto más cuanto que la larva puede pasar facilmente de una planta a otra. La *Pistia* se reproduce por estolones, y por eso hay siempre muchas plamtas reunidas sobre la superficie de las aguas donde vegeta."

I have since been able to confirm the findings of Lutz by collecting the larvae of *Lepidoselaga lepidota* from the base of the leaves of *Pistia* on a number of occasions in Panama. The larvae of this species sometimes occur in considerable numbers among the leaves of these plants when the latter are thickly massed on the surface of pools of stagnant water.

Lastly I wish to report the finding of *Tabanus unicolor* Wied., in association with this plant in the Canal Zone. In July, 1929, I visited a pool of water near Gamboa, C. Z., several times for the purpose of collecting mosquito larvae. This pool was about forty feet in diameter, with but very little current and protected from wind action by high banks on two sides. Nearly the entire surface of the water was covered with *Pistia* and other aquatic plants. On one trip I collected a number of larvae of *Lepidoselaga* and also three other larvae that were larger in size and of a different appearance. These three larvae were nearly mature and were raised to adults. Upon their emergence the flies were sent to the late Dr. James S. Hine for definite classification and were found by him to be specimens of *Tabanus unicolor.*

Summary

Observations made in various parts of the world have shown that a number of species of blood-sucking insects that are of concern to man and animals are found to be closely associated with the water lettuce, *Pistia stratiotes.*

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LAWRENCE H. DUNN

GORGAS MEMORIAL LABORATORY
PANAMÁ, R. DE P.

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STABILITY OF CLIMAX PRAIRIE AND SOME ENVIRONMENTAL CHANGES RESULTING FROM BREAKING *

J. E. Weaver and Evan L. Flory

University of Nebraska

Continued study of the great midcontinental grasslands of North America throughout a period of years has impressed the writers with the high degree of stability of the climax prairie. This phenomenon has been carefully considered in a study of the types of prairie in the Missouri Valley over an area of several thousand square miles centering in eastern Nebraska but including five neighboring states. Present studies on the deterioration of the prairie under the impact of grazing, and changes in edaphic and atmospheric environment with the breaking and cropping of the land have further emphasized the stabilizing influence of a cover of grassland.

Occurrence of Prairie Remnants

Considerable areas of native prairie, undisturbed except by annual mowing, still occur in the more recently settled states such as Nebraska and South Dakota, but in Missouri and Iowa where breaking began 80 or more years ago they are infrequent. In fact one may drive for miles through areas of cultivated lands where extensive fields of corn, wheat, alfalfa, and other crops thrive in the fertile soil formerly occupied by native grasses. But close search reveals relict tracts of tall-grass prairie 20 to 160 or more acres in extent where the native sod still remains intact. Their former subjection to grazing by herds of buffalo, elk, and other native animals has been replaced by annual mowing, usually during September. The fires started by lightning or deliberately set by the Indians to make travel easier and more secure, to furnish earlier grazing and better conditions for hunting, or for other purposes, have practically disappeared. What minor changes the mowing, absence of grazing, etc., have brought about are known only in part. With few exceptions they have been too small to impress greatly the pioneers. The prairies as

* Contribution from the Department of Botany, University of Nebraska, no. 86.

they are found today represent climax conditions and afford impressive lessons as regards stability.

Nature of Stability

Stability denotes a high degree of equilibrium between the vegetation and its habitat under the control of the existing climate. It does not preclude minor changes in the abundance of the constituent species. This regularly occurs from year to year as a response to the extremely irregular variations in the factors of the habitat-complex. The phenomenon, however, is often more apparent than real. The more important species are long lived and continuously present. They may be either less or more conspicuous because of their lack or abundance of flowering and fruiting, depending upon locally unfavorable or favorable conditions. Conspicuous fluctuations occur mostly among annuals or other relatively short-lived plants. Although the details of the pattern of the prairie mosaic may change, the shiftings are of minor importance. The relative constancy of the numbers of plants over a long period of time and the ordinary fluctuations within relatively narrow limits indicate the high degree of balance or stabilization. There are no great waves of emigrations, neither are there immigrations, for the prairie is a closed community and invaders, with rare exceptions, are excluded.

Resistance to Invasion

Large tracts of prairie are practically uninvaded by weeds except to the extent that trails or roads have been made through them or soil has been washed into the ravines from adjacent fields. Small subseres are frequently initiated as a result of the occupancy of local areas by stacks of hay. Gopher mounds may temporarily cover the vegetation; the burrows of badgers and other animals likewise cause disturbance. Here invading weeds temporarily find a home from which their offspring are soon expelled as the prairie species reclaim the soil. It is indeed impressive to find these relict areas of prairie entirely uninvaded, although surrounded on all sides by cultivated crops with their accompanying annual weeds or by pastures with their usually longer lived weedy flora. They are free from invasion although the kinds of invaders are numerous and their methods of competition diverse.[1] In fact the number of possible invaders is quite as large as the more important prairie species themselves. A recent list of the immigrant flora of Iowa alone contains 263 species (Cratty, '29). Shimek ('31) states that 265 species make up the bulk of the prairie flora of Iowa. Steiger ('30) found 237 species of prairie plants on a single section (640 acres) of land near Lincoln. Weaver and Fitzpatrick ('34) list about 50 grasses and grass-like species as being of considerable importance. They found approximately 142 species of forbs occurring in at least 10 per cent of the 135 prairie areas studied.

[1] *Poa pratensis* constitutes a notable exception. It has spread widely under annual mowing (*cf.* Weaver and Fitzpatrick, pp. 179 to 182, '34).

Small tracts of prairie, if undisturbed, are also remarkably free from invasion. Frequently strips of native prairie 10 to 20 feet wide, but miles in length, are found along railways. " In many cases these prairie strips have been preserved without appreciable deviation from the pure prairie type even where bordered on the one side by the roadbed with its ever-present belt of weeds, and on the other by farm lands which have been under cultivation from 30 to 60 years " (Shimek, '31). Similar areas are to be found along roadways throughout the more recently settled portions of the prairie region. Such small tracts of prairie, if undisturbed, contain all the species found in larger areas and the distribution is similar. But care must be taken not to place too much dependence upon them. If they have been grazed, very frequently burned, or otherwise disturbed in the past, the present flora of such localized areas may not be entirely representative of the prairie proper.

This is well illustrated by the absence of the genus *Psoralea*, and especially *P. floribunda*, from many apparently undisturbed prairies. In fact, in prairies only a half-mile away they may be abundantly represented. These legumes were perhaps entirely exterminated by grazing for a few years, after which the prairie, no longer pastured, " returned " without them.

Reestablishment of Prairie

Sometimes prairie land is broken, cropped for a number of years, and then left untilled. When cultivation is discontinued on land adjacent to prairie and the surface soil is not otherwise disturbed, the land " goes back " to prairie. The weedy annuals and perennials which constitute the early stages of the subsere are gradually replaced by the original prairie grasses and forbs. The rate of reestablishment varies greatly, the time for the occurrence of stabilization depending in a large measure upon the water relations, soil type, and especially the size of the denuded area. Drier years often lessen the effective competition of the ruderals and turn the balance in favor of the native flora. The area may appear like prairie after the passing of 7 to 15 years. The final equilibrium attained between species—as far as it is ever attained in nature—and the reestablishment of the former interrelations between vegetation and soil would probably require a much longer time.

Nature of Control

Control in grassland does not require complete occupancy. This is shown by the fact that the actual ground or basal cover seldom exceeds 25 per cent. It is usually about 15 per cent and in some of the densest types of grassland, such as *Spartina michauxiana*, less than 1 per cent. The control is exerted partly through competition for light, and especially for the water supply. In uplands the light values near the soil surface, such as are met by invading seedlings, often range from 20 to 60 per cent on days of full sunshine; under the dense cover of the taller lowland vegetation, from 1 to 10 per cent. One

needs only to examine a bisect in the prairie soil to fully comprehend how every cubic inch is permeated with the fine absorbing rootlets of the grasses to a depth of several feet. Intermixed with these and often extending far below are the root systems of the forbs. The root masses thoroughly occupy the soil continuously from year to year.

Determinations of soil moisture over a long period of years have shown that the prairie species frequently exhaust all the available moisture in the surface 6 inches of soil—the layer upon which the roots of seedlings must largely depend. The well established vegetation each year develops rapidly from accumulated food supplies, the taller grasses often growing a centimeter per day. During years of drought practically the entire available water supply is used. The prairie is a field with many crops; some are growing at all times from spring until fall. Blossoming and ripening of fruit is a continuous process throughout the growing season. If water is abundant, as in years most favorable to growth, the invading seedlings may share the supply only to be deprived of sunshine by the rank foliage of the native flora.

Stability is increased by the long span of life of many prairie species. Perhaps only about 5 per cent are annuals. The dominant grasses such as the Andropogons, *Sporobolus heterolepis*, etc., once established, retain their vitality many years. This has been determined by continuous observation, by long-time permanent quadrats, and by a study of the slow centrifugal growth of the bunches which only after many years disintegrate. It has been further confirmed by a study of seedling establishment over a period of years; many seedlings may appear, but few ecize (Blake, '34).

The climax vegetation is the outcome of thousands of years of sorting out of species and adaptations to the soil and climate. In fact, it is more than this, for the vegetation itself has had no small part in determining the physical, chemical, and biological properties of the soil. It has also reacted upon climate. The vegetation represents not only an evaluation of the present edaphic and atmospheric factors but also those of the past. Climax prairie is in close adjustment with its environment.

Unless disturbed by man, and barring the entrance of a new dominant from another region, the prairie will maintain possession until there is a fundamental change in climate or a new flora develops as the outcome of long-continued evolution.

Comparison of the Prairie Habitat with that of Cultivated Fields

With the breaking of the prairie and the growth of cultivated crops, the environment is profoundly modified. Under natural conditions the living prairie cover is renewed in early spring and throughout the entire growing season the grassland continuously presents a cover of foliage for the absorption of radiant energy. In fields with annual crops such as corn, wheat, oats,

rye, barley, and sorghums, the soil, for a time, is entirely bare. The grassland cover, viewed from above usually conceals from 60 to 100 per cent of the soil. This cover is very effective in absorbing the radiant energy since it usually consists of plants varying in leaf pattern and height, the foliage of which more or less overlaps. Often three to five more or less distinct absorbing levels occur. On a single square foot of lowland, for example, *Fragaria* or *Viola* may be overtopped by *Steironema* or *Anemone* and both by species of *Asclepias*, which in turn may be shaded by *Elymus* and the latter by *Andropogon.*

Even after mowing, the ground is not bare. The bases of the plants extend 2.5 to 3 inches high before new growth begins in autumn. A mulch of fallen leaves, fragments of stems, flowers and fruits, etc., forms a more or less continuous cover of varying thickness. This may have a dry weight of 50 to 225 grams per square meter on uplands and over 1000 grams on lowlands. Thus at all times the soil is protected from direct insolation. The maturing crop of corn may present a leaf surface four times as great as the actual acreage planted (Kiesselbach, '16), but this leaf surface is exceeded by that of the little or big bluestem by 50 to 100 per cent. In the field of wheat, the soil may be fairly well covered in spring but the crop is harvested by midsummer and, under the better farm practices, immediately laid bare by plowing. With crops of clover and alfalfa conditions more nearly approach those of the prairie, although here the accumulated foliage is almost entirely removed two or more times during the growing season.

The nature of the soil itself affects the reception of radiant energy on mowed prairie or on those where the cover of vegetation is less well developed. The prairie soil presents an excellent granular structure to a depth of 8–14 inches. Usually about 55 per cent by volume is pore space occupied by air and water. In fields long under cultivation this structure is much less evident and the soil is more compact. Prairie soil is always filled with living roots and rhizomes, decaying plant parts, and the network of channels left by them. Organic matter is high, often about 5 per cent by weight and very much more by volume in the surface six-inch horizon. Thus, owing both to the structure of the soil itself, but especially to its cover or lack of cover of vegetation, conditions for absorption of radiant energy are very different in cultivated field and native grassland.

Extensive comparisons of the environment and some physiological responses of prairie vegetation and cultivated corn (Flory, '34) and similar comparisons between prairie vegetation and wheat (Noll, '34) are under way in eastern Nebraska. The data to be presented here are preliminary measurements made by the writers and indicate some of the marked changes that occur when the native grassland is broken and cropped.

Light and Temperature

The relative energy relations, as expressed in terms of light, have been determined in fields of corn and adjacent upland prairie. At one-half the height of the vegetation, when the foliage cover has reached its maximum, the light is frequently only 65 per cent of full sunshine in cornfields and 25 per cent in prairie. At the base of the plants it is often 50 and 5 per cent respectively. These determinations were made by means of Clement's photometers.

The stabilizing influence of prairie as compared to cultivated fields on temperature is marked. Since the extremes are often more critical and significant to plants than are the means, an extreme case will be cited. On a cloudless day, June 10, 1933, during a period of intense heat and prolonged drought, the data in table I were obtained between 3:30 and 4:00 P.M. Both field and prairie were on Lancaster loam occupying a moderate north slope and only 500 feet apart. The air temperatures were taken in the shade of the body of the observer.

Table I. *Comparative temperatures in cornfield and prairie*

Place of Reading	Cornfield	Prairie	Difference
Air, ht. 4 ft.	106° F.	102° F.	4° F.
Air, ht. 4 in.	111	100	11
Air, at soil surface	124	103	21
In soil surface	136	98	38
Soil, depth 3 in.	114	94	20
Soil, depth 12 in.	84	81	3

The marked differences in air temperatures reflect themselves both in greatly decreased humidity and increased transpiration. The increase in soil temperatures not only has a profound effect upon promoting water loss from the soil, and directly upon root functions, but also upon the activities of microorganisms. While nitrate production, for example, proceeds at a maximum rate in the moist prairie soil at 94° F., at higher temperatures it becomes slower and may cease altogether at 131° (Russel *et al.*, '25).

At a depth of 3 inches, the mean soil temperature in the cornfield during three consecutive growing seasons was 8.3° F. higher than in the prairie. Even at a depth of 8 inches an increase of 2.2° occurred (Flory, '34).

Humidity

Temperature has a profound effect upon atmospheric humidity. In general one degree Fahrenheit rise in temperature decreases the humidity 1.5 to over 2 per cent depending upon the locality. Extreme differences in humidity in field and prairie are often surprisingly great. During the day cited, which was typical for a twenty-day period in June, the relative humidity at a

height of four inches in the prairie was 31 per cent. It was only 12 per cent 4 inches above the hot, nearly bare soil in the field of corn. Over the cornfield, even at a height of four feet, the humidity was only 15 per cent as compared to 20 per cent in the prairie. A lower mean daily humidity in the cornfield prevailed throughout three growing seasons, and the mean day humidity was approximately 5 per cent higher in the prairie.

Comparative measurements of humidity and temperature were made just above a 20-acre field of alfalfa and in a similar adjacent field where the crop had been harvested. The living plant cover increased the humidity 10 per cent and lowered the temperature 4° F.

Wind

Mid-continental winds are practically always dry. A comparison of wind movement at various heights from the top of the foliage to the surface of the soil showed that in the prairie it was always less. Except on extremely windy days air movement beneath the dense foliage of grasses and forbs was not marked. Frequently there was none. A breeze of 9 miles per hour three feet above the surface of the prairie vegetation was reduced to 3.7 miles at the height of the foliage and to .1 mile at one-half this height. At the soil surface there was none. In the field of corn wind velocities at corresponding heights were 8.5, 5, 2.5, and .9 miles per hour respectively. These measurements were made late in July when both prairie and corn had produced their maximum foliage. Wind movement among the corn plants at any time was greatly in excess of that among plants of the prairie.

Evaporation

Livingston's white, spherical atmometers were employed in comparing relative water losses in field and prairie. Average daily evaporation rates from July 15 to 24 are shown in table II.

Table II. *Evaporation losses at various heights*

Place of Reading	Cornfield		Prairie		Per cent increase in field
	Height	Evaporation cc.	Height	Evaporation cc.	
3 ft. above plants	9 ft.	55.7	4.25 ft.	55.3	0.7
At height of plants	6 ft.	42.3	1.25 ft.	33.3	27.0
One-half ht. of plants	3 ft.	31.1	7.5 in.	15.1	106.0
Near soil surface	3 in.	22.5	3.0 in.	13.4	68.0

The increase in the rate of evaporation of 27 to 106 per cent at various levels within the cultivated field is clearly of sufficient magnitude to be of great significance as regards rate of water loss in a dry climate.

The increase in evaporation rate from similar pairs of atmometers placed near the soil surface was 80 per cent greater in a closely grazed pasture than in an immediately adjacent prairie.

Transpiration

The behavior of plants themselves in different habitats is of greatest importance since here the living organisms are responding to the total impact of the environment. Cylindrical cores of undisturbed prairie sod 5 inches in diameter and 18 inches deep were enclosed in metal cylinders which were sealed at the base. Corn was grown for three weeks in containers of appropriate size, which were sealed at the beginning of the experiment. Both the native and cultivated grasses were placed at the general level of the surrounding vegetation.

The average losses of the corn in its field and the prairie respectively were .34 and .18 grams per square centimeter of leaf surface. Those of the little bluestems were .36 and .30 grams. Thus under field environment the average loss from the several corn plants in excess of the average losses in the prairie was 89 per cent. Transpiration from the bluestem was increased 20 per cent when placed in the field of corn. During the same 10-day period in the latter half of July, the evaporation in the cornfield was 36 per cent in excess of that in the prairie. Thus the increase in light, temperature, wind movement, and evaporation and the decrease in humidity in the field have a profound effect upon the rate of transpiration.

The Soil in Relation to Water

Turning attention to the edaphic conditions, it should be pointed out that even if the actual precipitation is not decreased under annual cropping (and this may be found to be the case) certainly the distribution of water is more uniform over a prairie than over an area that is annually denuded. The snow lies much more uniformly and is less drifted by the wind in the tall-grass prairie and run-off resulting from heavy rains is much less. When rains occur, and especially the torrential ones characteristic of the dry prairie climate, the water does not beat directly upon the soil. Instead its force is broken by the cover of foliage and by the ever present surface mulch.

In the cultivated field, upon areas where the soil is bare or only partially covered by the growing crop, the raindrops beat upon the soil like millions of little hammers. The soil is compacted. The cohesive force between the soil particles is lessened as the surface becomes muddy. They shift their positions under the effect of the beating rainfall and fill up the soil pores. Thus the absorbing capacity is reduced. The excess water accumulates on the surface and on running off removes with it the surface soil particles, the humus and the dissolved salts. But in the prairie the soil is more receptive to water, since its structure has not been destroyed by cultivation, its organic content

lessened by cropping, nor the network of roots and rhizomes, which thread it everywhere, annually destroyed.

The pore space in the upper 6 inches of a fairly mature upland prairie soil (Lancaster loam) was 50.5 per cent. This was decreased over 12 per cent within 6 years after the prairie was broken and continuously cropped to corn. Water penetration into this field soil was found to be only 60 per cent as rapid as into the unbroken prairie sod.

Run-off and Erosion

Run-off in the prairie is usually slight unless the rains are heavy. Abundant humus creates a sponge-like condition in the top soil which increases its capacity to absorb and hold water, thus decreasing run-off. The water that does run off is usually clear, since the soil is firmly held in place by the bases of the plants, their widely and deeply spreading root systems, and the protection afforded by the soil mulch. The litter retains a half liter or more of water per square meter when it becomes saturated. This amount is insignificant in terms of soil moisture. The lodgement of the undecayed material between the stems of grass, however, forms an intricate series of minute dams and terraces which tend to hold the water until it can percolate into the soil. Surface erosion and gullies are not features of the prairie. It is only when the vegetation is closely grazed, and thus the amount of roots and rhizomes diminished that serious erosion begins. Trampling of the soil is additionally detrimental. On steep hillsides of similar slope two years of close grazing increased the run-off 50 to 80 per cent. Losses of valuable soil by excessive erosion are steadily impoverishing and even destroying vast areas of crop and grazing lands throughout the United States.

In a field planted to winter wheat a rain of 2.7 inches fell on a 4 degree slope during a period of two days early in December. Although the wheat had made an excellent fall growth, the run-off from 100 square feet of the dry, unfrozen soil was 38 per cent greater than on a similarly enclosed area of mowed prairie only a few yards distant.

Notwithstanding the increased run-off, the prairie farmer who left his " sloughs " and ravines to their natural cover of *Spartina* or other grasses has not had his farm cut into separate fields by deep, impassable gullies. He is also still able to secure yearly from these lowlands two or three crops of hay. In the old pastures and especially in the cultivated fields the annual losses of top soil by erosion are very great. When the soil is loosened by the plow, and especially when it gets into a poor physical condition as a result of long cultivation, it is often easily eroded both by wind and water. Fortunately sowing the soil to grass is a method of holding it in place. It is also a method of restoring to old, worn out soils the productivity and good tilth of virgin ones. The maintenance of an adequate supply of organic matter under climatic conditions indicated by prairie is very essential from the standpoint of

water-holding capacity; supplying energy materials necessary to the bacterial flora concerned in nitrogen fixation; and in preserving the crumb structure which resists blowing away of the soil.

Relative Demands for Water

The actual available water-content of the soil in prairie and tilled fields of various crops and the relative demands of the natural vegetation and crop plants upon it should be determined. The prairie vegetation, rooted throughout several feet of soil, begins growth early in spring. The field for corn, on the contrary, lies fallow. Planting time occurs in May and the new crop may absorb only in the surface foot until well into June. The prairie continues growth notwithstanding drought in the surface soil, drought that may be so severe as to check greatly the growth of the new corn. With the progress of the season, the need for more and more water by the developing foliage in the prairie increases. This is in accord with the annual rainfall which usually reaches a maximum in June or July. These demands do not all occur at the same soil level. They are met in part by direct absorption from the soil even far below 5 feet. By midsummer a maximum transpiring area has been attained by the dominant grasses; the increase of water demands by the still growing autumnal forbs are probably largely offset by the waning or disappearance of vernal or estival species. Not so in the field of maize. The need for water constantly increases until flowering and fruiting. Roots are rapidly extended into the deeper soil—into the third, fourth, and fifth foot, which heretofore has furnished little or none of the supply. The demands for water are great and urgent. Actually these deeper soil layers are more depleted of their moisture early in autumn than are the corresponding ones in prairie.

Water relations in a field of winter wheat are quite different from those in either cornfield or prairie. Beginning growth in the surface layer in early fall, the wheat roots often reach a depth of 3 or 3.5 feet before growth is retarded or ceases because of low temperatures (Weaver, Kramer, and Reed, '24). In spring, resumption of growth precedes that in the prairie, and the maximum demands for water—by all plants at the same levels—precedes that in the grassland. By midsummer it ceases abruptly.

The effect of the prairie upon fertility and the resulting demands for water is exerted even after the native vegetation has been destroyed by plowing. The soil for a few years is mellow, moist, and rich, and produces abundant crops. Unlike the soil of plowed fields of alfalfa, the nutrients are liberated gradually. There is no overstimulation of the crop because of an excess of nitrogen and the accompanying intensification of periods of drought.

Need for Comparative Study of Natural and Field Environments

There is a real need for a study of the prairie environment in comparison with that of cultivated fields. Soon the native prairie will be gone forever. Undoubtedly important changes in atmospheric humidity, regional loss of water by run-off, and lowering of the water table have already occurred. It seems clear that the more general influences of prairie climate may have already been modified by extensive cropping. Environment in limited and detached areas of native grassland, however, is still not far different at least in its micro-climate from the time when these areas were a part of the apparently unending sea of grassland.

A thorough study of Nature's crops and Nature's way of making the most of a sometimes adverse environment is of scientific importance. It is also fundamental to an understanding of the effect of prairie upon stabilizing such factors as temperature and humidity, and its effect upon stabilizing the soil. It furnishes a basis for measuring the degree of departure of cultural environments from the one approved by Nature as best adapted to the climate and soil.

The prairie crop is a mixed stand. Various legumes are blooming or ripening fruit from April until October. The same is true of the different species of grasses. There is a time for flax, another for mints and still another for roses. Not all of these crops are bountiful every year. Some may form no viable seed. Indeed there is no pressing need among the perennials for fruiting each year. Only on wet years does little bluestem normally fruit abundantly on dry uplands. How unlike the more delicate, annual crops of man. Neither is there a critical time for drought as in wheat, or corn, or clover, where a few days of adverse conditions may prove disastrous. Height and density of cover vary annually as does also the tonnage of hay. If drought comes early, growth is resumed upon the advent of wet weather. If it comes later, the earlier yielding prairie components have had a good year. Nature's crops are adjusted to fit into periods of dry cycles as well as wetter ones. These have recurred again and again throughout the centuries. Reserves of food of native plants are extensive and their resources for obtaining water excellent.

Cultivated plants are affected more readily by extremes of environment. Corn, for example, germinated well during 1933 and the early growth was rapid. Lack of rainfall before the phase of enlargement seriously threatened the crop. Heavy rains during this phase of growth produced unusually tall plants. During the dry early summer there were only a few times when the seeds of Sudan grass germinated. During drought in August the crop exhausted the available soil moisture even on low ground and ripened seed prematurely. The adjacent prairie grew continuously, however, and gave a good yield of hay.

These examples illustrate dangers of losses incurred in cropping. They

are a part of the price civilized man pays for replacing the stable crop evolved by Nature by the unstable ones he selects. Crop production is essential to civilization and inevitable if the race is to endure. Nowhere in North America is the soil more favorable for crop growth than in the tall-grass prairie, although sufficient water often becomes a limiting factor, especially in the western part. It seems clear that a knowledge of the degree of departure, in growing each kind of crop, from the mean established by Nature is highly desirable.

The excessive demands of certain crops upon the prairie environment have just come to be realized. In native prairies the deeply rooted legumes and species of similar habit are relatively widely spaced. Under cropping conditions, however, the deeply rooted alfalfa is grown in dense stands. Frequently it so thoroughly depletes the upland subsoil of its moisture that it is difficult or impossible to grow again alfalfa, even after a lapse of a score of years, on soils thus drained of their water supply. When all the fields of a farm have once been enriched by crops of alfalfa and at the same time depleted of their subsoil moisture, the problem of maintaining soil productivity may become a very difficult one (Kiesselbach. Russel and Anderson, '29). While some consider this sapping of the subsoil a clever method of utilizing the natural resources in a dry climate, others are of the opinion that it may have an unfavorable reaction in lowering the water table and in the drying up of springs and streams. Both phenomena have resulted from disturbing Nature's balance by breaking and cropping the land with its attendant run-off and erosion.

What are the relations of the various crops such as sorghums, oats and wheat to their new prairie habitat? Are the requirements of these and other crops within the limitations of prairie climate and soil, or are they demanding more, under present methods of cropping, than the habitat has to offer? Are we properly utilizing Nature's prairie garden or exploiting it?

A survey of agricultural progress in America shows that in many cases we have not used our lands wisely. In the humid east much land in forest should not have been cleared. In the semiarid west vast areas of range lands should never have been broken. In the development of scientific programs of land utilization there is great need of sorting out the various eroded or otherwise unproductive lands to be put again under a protecting cover of forest or grasses. As pointed out by Lipman ('32) these lands "not being in themselves profitable, are only a menace to the welfare of those who are trying to use profitably land which is legitimately agricultural."

Upsetting the Balance of Nature

After only half a century of prairie farming, soil investigators are greatly concerned with the rapid changes in soil fertility, structure, and water relations. We have not fully reckoned with the climatic factor in its relation to

the building and conservation of soil fertility. Many other factor changes may well cause concern. What will be the penalties for disturbing Nature's balance?

The relation of the modified soil temperatures in bared areas—extremely high by day and lower than normal by night—to microorganisms has already been mentioned. Drying the surface a little more by removing the cover of vegetation, the mulch, and their shade will greatly change bacterial activity as well as that of other soil flora and fauna. An open field can not shelter in its upper layer the same population of microorganisms as can a shaded soil under the prairie grasses. Opening the stand and intermittently baring the ground establishes a new and little understood relation to light, temperature, humidity, and wind. Such modifications offer new and diverse environments. The upset of the long established equilibrium starts an extremely complicated series of changes. These include the relation to the environment of disease producing organisms of both plant and animal origin. The relatively hardy and disease resistant flora of the prairie is at the same time replaced by one more tender and more varied in its susceptibility to disease.

Smith ('32) has recently pointed out some penalties for upsetting the balance of Nature in the prairies and plains. He states that insect and plant-disease problems caused by a modified fauna are actually increasing, both in number and severity. He concludes that man, the disturber, will have to employ artificial control efforts for a long period, or be seriously handicapped in his labors.

The increase of the rabbit population on overgrazed as compared with stabilized areas and a similar change in the abundance of the striped ground squirrel may be cited as examples of a disturbed natural balance. Various other rodents and ants probably occur in grasslands in larger numbers in consequence of overgrazing, surface erosion, or other disturbance. Under these conditions the tough sod disappears and the soil is more easily loosened. Rabbits, prairie dogs, and other rodents very much prefer the more succulent forbs, that are so plentiful in disturbed areas, to the climax grasses (Schaffner, '26, Vorhies and Taylor, '33). Overgrazed areas, more weeds and more rodents go hand in hand. The pocket gopher thrives and enormously increases in abundance, living upon the roots of alfalfa, and aided by the farmer who destroys his natural enemies. Returning in numbers to his native home, the prairie, he becomes a great disturber. Frequently ten times as many insects are obtained from grazed as from adjoining ungrazed areas.[2] In fact, climax grassland offers a barrier to many species. Grasshoppers oviposit in bare soil and find conditions for growth, as do also white grubs, far more congenial in overgrazed areas (Fluke *et al*, '32). Similar changes resulting from the close grazing of prairie or the breaking of the sod are legion.

The great dust storms are an increasing menace and give cause for reflec-

[2] From correspondence with Dr. A. O. Weese.

tion. Even if the millions of acres of bared soil do not promote convexion currents and consequent wind movements, certainly they do furnish the tons of dust that are carried in the atmosphere for miles and finally deposited in neighboring states.[3] Great winds have probably always been prevalent in the prairie but not clouds of dust that darken the sky!

With the weakening or removal of the prairie sod, the menace of erosion is ever present. What in detail are its relations to the various systems and degrees of grazing? Under cultivation, the top soil from many hills has already been eroded until only the lower slopes and level crowns of the hills can be profitably farmed. Shall we await the arrival of the fertile soil from the slope to be held in the valley by the brush dam or other device or shall we forestall its removal by applying Nature's remedy of a permanent cover of vegetation on the steep hillsides? Since plant ecology is a study of the plant and of vegetation—native or otherwise—to its environment, surely these problems should vitally interest the ecologist.

The applications of lessons learned from a careful study of vegetation are manifold. In this period of the reclaiming of marginal lands, of planning great projects to ameliorate erosion, of developing scientific plans for land utilization, and of definite planning to establish cropping systems best calculated to produce economic returns from the different types of soil, we may profitably consider the natural environment. Not until the native environment in its relations to water, humidity, temperature fluctuations, and other critical factors of both air and soil has been compared with that of overgrazed and cropped areas will it be known how widely we are departing from Nature's plan of a stable environment. Such comparative studies should be made now, before the opportunity with the destruction of the natural vegetation has forever passed.

The writers are indebted to Prof. J. C. Russel and Dr. Herbert C. Hanson for reading the manuscript.

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A CRITICAL DISCUSSION OF VARIOUS MEASURES OF OXYGEN SATURATION IN LAKES

W. E. Ricker

Pacific Biological Station, Nanaimo, B. C.,

Biological Board of Canada

From the time of the earliest studies of the gases dissolved in lake waters, investigators in this field have been in the habit of comparing observed quantities of oxygen with some standard value, which they think such water should contain, or would contain if certain stated conditions were fulfilled. The difference between the standard and the observed value is known as the *oxygen deficit*, and may be expressed in absolute units (cubic centimeters per liter or milligrams per liter), or as a percentage of the standard. One hundred times the observed value over the standard value is usually known as the *percentage saturation* of oxygen in the water, which term is rather loosely used in this connection.

Solubility Tables

Since all standards which have come to the author's attention are based upon some form or other of oxygen solubility table, these should first be considered. If oxygen were the only important gas in the atmosphere, the problem would be much simplified. As it is, with oxygen in the atmosphere, there are nitrogen, argon, water vapor, and small quantities of other gases, notably carbon dioxide. The solubility of oxygen from the air in water at 760 mm. total pressure, *i.e.*, the quantity of oxygen contained dissolved in water which is in gaseous equilibrium with the atmosphere at 760 mm. total pressure, will vary as the partial pressure of oxygen in the atmosphere, which in turn will vary as the proportion, by volume, of oxygen in the atmosphere. As regards the "permanent" gases, the atmosphere is of almost unvarying composition, the ratio of oxygen : nitrogen : argon = 20.9 : 78.15 : 0.95. On the other hand, the quantity of water vapor present varies in an irregular and usually unpredictable fashion. In the case under consideration, when equilibrium has been established with respect to the processes of oxygen dissolving and coming out of solution, there will also be equilibrium with respect to the processes of water vaporizing and condensing, *i.e.*, the atmosphere in contact with the water will be saturated with water vapor. The proportion of water vapor in a saturated atmosphere, and hence its partial pressure, of course increases with temperature; this fact must be borne in mind when considering the saturation tables now in use.

A good number of chemists have made observations upon which oxygen solubility tables have been based, and at least four of these have been used

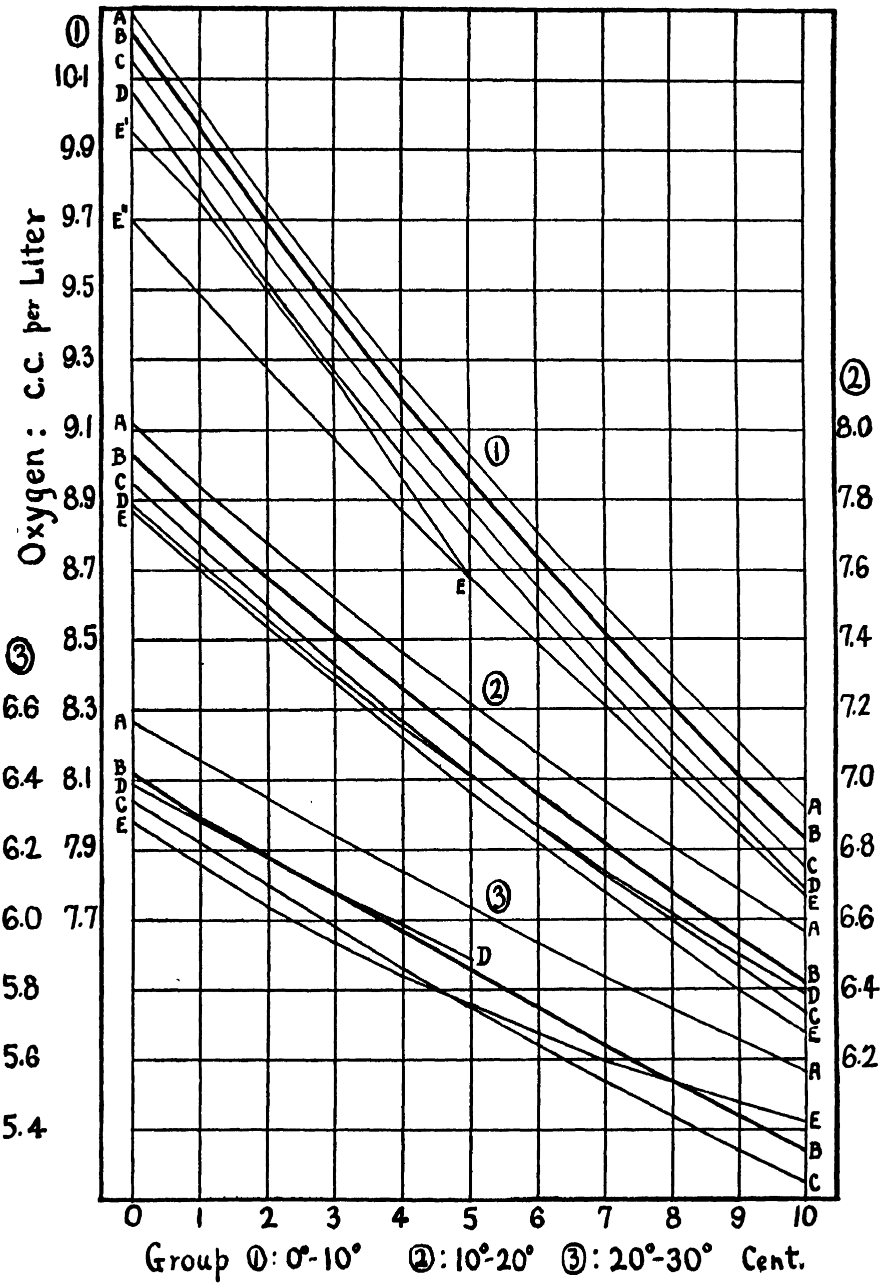


FIG. 1. Comparison of oxygen solubility tables. *A*: Birge and Juday, '14. *B*: Whipple and Whipple, '11. *C*: Winkler, '89. *D*: Jacobsen, '21. *E*: Roscoe and Lunt, '89. *E'*: Sutton, '24. *E''*: Whipple and Parker, '02. Group 1: 0°–10°, 2: 10°–20°, 3: 20°–30°.

by limnologists, *viz.*, those of Roscoe and Lunt ('89), of Fox ('07, '09), of Winkler ('89) and of Jacobsen ('05, '21) (fig. 1). The table of Roscoe and Lunt is one of the oldest. In its original form it covered the range 5°–30° in intervals of 0.5°. "In this table results are not calculated for aeration at a *dry* pressure of 760 mm., but for an observed barometric pressure of 760 mm.," say the authors. Birge and Juday published and used this table in their Wisconsin work of 1911, interpolating values at every tenth-degree, and using the extrapolated values of Whipple and Parker ('02) for the 0°–5° range. It is also to be found in Report Ontario Board of Health ('20) and in Sutton ('24). The last named author prints an accessory table, based on his own observations, to cover the 0°–5° range. Although Birge and Juday later abandoned this table, their version of it was used as lately as 1928 by Thienemann, in his very complete analysis of the occurrence of oxygen in lake waters. It has been used too for standardizing reagents for many of the determinations made by the Ontario Fisheries Research Laboratory, and Sutton's version was used throughout the published work of the present author ('32, '34).

The observations of Fox ('07, '09) are available in two forms. Fox's original data give the "absorption coefficient" of oxygen, the quantity of oxygen dissolved by water from an atmosphere of pure oxygen, when the pressure, *exclusive of water-vapor*, is 760 mm. Birge and Juday ('14), publish a table calculated from this, showing "the number of cubic centimetres of oxygen absorbed by 1 liter of distilled water at different temperatures from a free dry atmosphere of 760 mm. pressure." Actually, water can never exist in equilibrium with a dry atmosphere; these tabulated values therefore indicate greater quantities than would be dissolved from a saturated atmosphere, the discrepancy ranging from 0.5 per cent at 0° C. to 3.7 per cent at 30° C. Although the table is one of absorption coefficients rather than solubilities *sensu stricto*, it has nevertheless been widely used, in all Birge and Juday publications from 1914 to the present, by Clemens for calculating percentage saturations from his lake Nipigon data, by Alsterberg, Lönnerblad and other Swedish workers, and doubtless many others throughout the world.

Wereščagin, Aničkova and Forsch ('31, p. 18) publish a table calculated in similar fashion from Fox's data, values being in mg. per liter. It is unfortunate that they failed to make the necessary adjustment for water vapor tension, as their paper is published as one of the works of the committee on standardization of the International Association for Theoretical and Applied Limnology.

Whipple and Whipple ('11) give another version of Fox's data. These authors originally set out to construct a table from their own experimental data, but finding these to be practically identical with the earlier work, contented themselves with bringing his results into a convenient form for the use of hydrologists. An abbreviated form of the table is published on page

62 of Standard Methods for the Examination of Water and Sewage, 5th Edition, figures tabulated being in parts per million; it shows "the solubility of oxygen in fresh water . . . at various temperatures when exposed to an atmosphere containing 20.9 per cent of oxygen, under a pressure of 760 mm." (including water vapor). In limnological work, this table has been used by the chemists engaged in the surveys of the New York State Conservation Department.

A third set of observations was made by L. W. Winkler ('89); they may be found in Landolt-Börnstein's Physikalisch-chemische Tabellen, 5th Edition, Vol. I, p. 764, and in essentially the same form, as Dr. N. A. Lange informs, in the Handbook of Chemistry and Physics, 14th Edition, p. 538. Two values are tabulated: "α, the absorption coefficient is the volume of gas reduced to 0° C. and 760 mm. absorbed by one volume of water, when the pressure of the gas itself, without the aqueous tension, amounts to 760 mm." These values, multiplied by 1,000 times the volumetric fraction of oxygen in dry air, give a table comparable to that calculated by Birge and Juday ('14) values being in cubic centimeters per liter. Included also is "q, the weight of gas in grams, dissolved in 100 grams of water when the total pressure (*i.e.*, the sum of the partial pressure of the gas plus the aqueous tension at the given temperature) is 760 mm." These values, multiplied by 10,000 times the fraction by volume of oxygen in dry air, give a table comparable to that calculated by Whipple and Whipple ('11), values being in milligrams per liter (= parts per million, in fresh water of the temperature range under consideration). Maucha ('31) uses this table for limnological purposes and claims it is "äusserst genau"; in a later work ('32, p. 21) he publishes it, calculated in convenient form.

The solubility table of Jacobsen ('05, '21) covers the range 0°–25° C. It shows "la quantité d'oxygène, mesurée à température 0° C. et à la pression 760 mm. qui peut être absorbée dans l'air atmosphérique par litre d'eau . . . , la pression atmosphérique (sans vapeur d'eau et sans acide carbonique) étant 760 mm. de mercure." It is therefore open to the same objection as is that of Birge and Juday ('14); in nature at least, oxygen is dissolved from a saturated rather than a dry atmosphere. It has been used by some marine chemists, and in the Irish limnological work of Southern and Gardiner.

It is desirable that limnologists should adopt one of these tables universally. That of Roscoe and Lunt has been widely used, and that of Birge and Juday ('14) is perhaps even better known. To the author it seems that both of these must be ruled out, the first because of the uncertainty of the 0°–5° range, the last because it is theoretically unsound for this work, as is also the case with Wereščagin's version. Jacobsen's table has both these defects, though in this case it is values above 25° which are lacking. Of the two remaining, that of Whipple and Whipple is most recent, is calculated from observations made with more modern technique, and is set forth in most convenient form for this work. It also has the support of sanitary engineers,

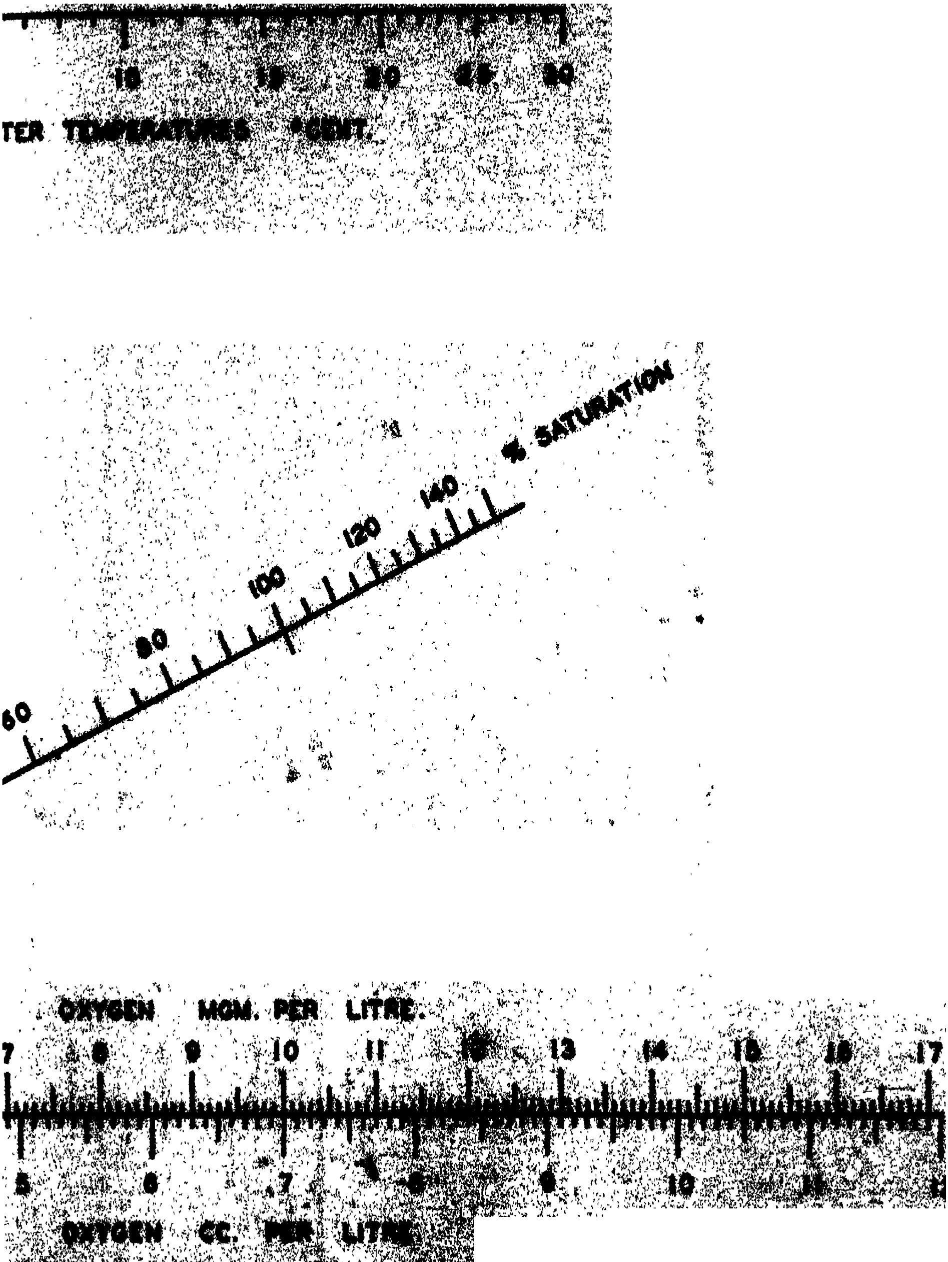
and of most marine chemists,[1] because alongside distilled water solubilities are tabulated solubilities of atmospheric oxygen in salt solutions of various concentrations.

TABLE I. *Solubility of oxygen from an atmosphere containing 20.9 per cent oxygen by volume, and solubility (q) of oxygen, atmospheric nitrogen, and carbon dioxide from an atmosphere of the pure gas, the total pressure (gas + vapor) being 760 mm. in all cases. Values for oxygen copied and calculated from Whipple and Whipple ('11). Values for nitrogen calculated from data of Fox ('09), being 1.017 times his absorption coefficients, corrected for vapor tension of water. (To change from cc. at N.T.P. to mg. of* pure *nitrogen, multiply by 1.251; of* atmospheric *nitrogen, by 1.257; of* dissolved *nitrogen, by 1.267.) Values for carbon dioxide are those of Bohr ('99), as given in Handbk. Chem. Phys.*

Temp.	Oxygen from normal atmosphere mg. per l.	Oxygen from normal atmosphere cc. per l.	Pure oxygen mg./l.	Pure "atmospheric" nitrogen[2] cc./l.	Pure carbon dioxide mg./l.	Temp.
0	14.62	10.23	70.0	23.3	3346	0
1	14.23	9.96	68.1	22.8	3213	1
2	13.84	9.69	66.3	22.3	3091	2
3	13.48	9.44	64.5	21.8	2978	3
4	13.13	9.19	62.8	21.3	2871	4
5	12.80	8.96	61.3	20.8	2774	5
6	12.48	8.74	59.7	20.4	2681	6
7	12.17	8.52	58.2	19.9	2589	7
8	11.87	8.31	56.8	19.5	2492	8
9	11.59	8.11	55.5	19.1	2403	9
10	11.33	7.93	54.2	18.7	2318	10
11	11.08	7.75	53.0	18.3	2239	11
12	10.83	7.58	51.9	17.9	2165	12
13	10.60	7.42	50.7	17.5	2098	13
14	10.37	7.26	49.6	17.2	2032	14
15	10.15	7.11	48.6	16.9	1970	15
16	9.95	6.96	47.6	16.6	1903	16
17	9.74	6.82	46.6	16.3	1845	17
18	9.54	6.68	45.7	16.0	1789	18
19	9.35	6.55	44.8	15.7	1737	19
20	9.17	6.42	43.9	15.5	1688	20
21	8.99	6.29	43.0	15.2	1640	21
22	8.83	6.18	42.2	14.9	1590	22
23	8.68	6.08	41.5	14.7	1540	23
24	8.53	5.97	40.8	14.5	1493	24
25	8.38	5.86	40.1	14.2	1449	25
26	8.22	5.75	39.4	14.0	1406	26
27	8.07	5.64	38.6	13.8	1366	27
28	7.92	5.54	37.9	13.6	1327	28
29	7.77	5.44	37.2	13.4	1292	29
30	7.63	5.34	36.5	13.2	1257	30

[1] During the Fifth Pacific Science Congress held at Vancouver in 1933, a committee of oceanographers recommended that Whipple and Whipple's version of Fox's data be accepted as standard.

[2] "Atmospheric" nitrogen is the name given to a mixture of 98.815 per cent vol. of nitrogen, and 1.185 per cent vol. of argon. The solubility of argon is slightly greater than that of oxygen, and more than twice as great as that of nitrogen.



for obtaining saturation values at normal pressure.

The fresh-water values only are set forth in table I of this paper. (Included also are the solubilities of oxygen, nitrogen and carbon dioxide respectively, from atmospheres of the pure gases.) Also, there is published herewith (fig. 2) a nomogram, constructed from the same data by Dr. D. S. Rawson of the University of Saskatchewan, from which saturation values (at normal pressure) may quickly be obtained. A black thread held so as to join the observed temperature with observed oxygen values on the upper and lower scales respectively indicates the correct saturation value on the middle scale.

This problem of selecting a table has a bearing upon the method employed in making oxygen determinations. The various distillation methods, employed by Birge and Juday ('11, in part) and some earlier workers, have now been completely superseded by two titration methods. That of Miller is quick and convenient for field work, but is usually considered less accurate than the iodometric method of Winkler. Miller recommends that final standardization of the ferrous ammonium sulphate used in titration be done by performing tests upon air-saturated water, and referring to a solubility table. In Winkler's method there is a choice between using for standardization, either (*a*) re-sublimated iodine, (*b*) potassium bichromate, (*c*) potassium bi-iodate or (*d*) water saturated with air. The first substance requires an analytical balance, hence for many is out of the question. The second has seemed unsatisfactory to the author and others, following various tests. The last is more troublesome than the others, but requires no apparatus or chemicals not used in the routine determinations. When daily variations in atmospheric pressure have been determined and applied in the calculations (*v.i.*) consistent results have been obtained. For a description of Winkler's method and its various modifications, see Maucha ('32) and Wereščagin ('31).

If the differences between the various saturation tables were proportional throughout, the same percentage saturation could be calculated from any one of them, provided the saturation method were employed for standardizing reagents. The differences are of course not strictly so (fig. 1), yet this fact argues in favor of the saturation method of standardizing reagents.

Barometric Pressure

All solubility tables are made out for an atmospheric pressure equivalent to 760 mm. of mercury, which is normal at sea level. Juday ('15) was perhaps the first limnologist to point out that solubility decreases with increasing elevation, to an extent of about 1 per cent for each 82 meters, although he did not include the correction in calculating his tabulated saturations at that time. Kemmerer, Bovard and Boorman ('23), in exposing their extensive observations on northwestern lakes of the United States, applied such a correction in the case of some mountain lakes whose elevation was known. They used table 25 of the Smithsonian Meteorological Tables. Among European

workers, Alsterberg ('29, etc.) and his Swedish colleagues have made allowance for decrease in pressure with elevation, as has Maucha ('31).

The basic formula used in finding the normal atmospheric pressure at a given elevation, and quoted in various forms by Alsterberg, Maucha and Geddes ('21), is:

$$h = 18400 . \frac{T}{273} . \log p_0/p \tag{1}$$

or,

$$\log p = \log p_0 - \frac{273h}{18400T}, \tag{2}$$

where h is the elevation of the station in meters,
p is the atmospheric pressure at that elevation,
p_0 is the atmospheric pressure at sea level,
T is the average absolute temperature of the column of air between the station and sea level.

Various authors variously dispose of the temperature term $T/273$. Maucha neglects to say what T is. Juday and Birge ('32), quoting Maucha's formula, say that t ($= T - 273$) is the temperature Centigrade of the surface water of the lake. Since this is usually about equal to the daily average air temperature in the vicinity at the time, it is a good approximation. In working on streams, or with any water in close contact with the air, it is better to put $t =$ air temperature at the time samples are taken. Alsterberg ('29, '30), in calculating his normal pressures, puts $T = 273$ (or $t = 0$), which amounts to an assumption that the mean temperature of this imaginary column of air was 0° C. at the time of the vernal overturn.

When working at high altitudes, the formula above might be somewhat modified. Geddes ('21) remarks that air temperatures decrease 1° C. for each 200 meter increase in elevation, as a rule. If T^1 be the absolute temperature of the air at elevation h meters, then

$$T = T^1 + h/400. \tag{3}$$

Substituting in (2):

$$\log p = \log p_0 - 5.934 \frac{h}{400T^1 + h}. \tag{4}$$

At 2,000 meters, the error involved in using formula (2) as an approximation for (4), with $T = T^1$, is only 0.46 per cent. At ordinary elevations it is quite negligible. Table II shows normal air pressure from sea level to 4,000 meters in 100 meters intervals, calculated from (4).

TABLE II. *Normal air pressure in millimeters of mercury at various elevations, when temperature at that elevation is 0° C. ($T^1 = 273$).*

Elevation Meters	0	100	200	300	400	500	600	700	800	900
0	760	750	741	732	723	714	705	696	687	697
1000	671	663	655	647	639	631	623	615	608	601
2000	594	587	580	573	566	560	553	546	539	533
3000	527	521	515	509	503	497	491	485	480	474
4000	469									

Having obtained the normal atmospheric pressure at elevation h meters, $= p$ mm., solubilities at that elevation may be calculated by multiplying tabulated solubilities by $p/760$. When any considerable number of observations on one lake are to be treated, it is easiest to calculate a complete table of solubilities for its elevation.

In standardizing reagents by the saturation method, it is not enough to know *normal* pressure at the elevation in question. What is wanted is the " instantaneous " pressure, *i.e.*, the pressure at the time the determination is made. If a good barometer is available, this may be obtained directly. If not, weather bulletins such as are published by the Canadian Meteorological Service or U. S. Weather Reports may be consulted. From them the pressure may be read to the nearest tenth of an inch of mercury, and as at sea level. It must be converted to the elevation in question by using formula (2) or (4) above.

If analyses are to be made of streams or rivers, this instantaneous pressure should always be used in calculating the saturation standard, rather than normal pressure, because river waters are frequently in contact with the air, and hence sensitive to daily fluctuations in its pressure. This has been done by the author ('34) in work upon Ontario streams; and the same treatment was uncritically applied to a few lake series taken at the same time (Ricker, '32). But since lake water, even that in the epilimnion, comes into direct contact with the atmosphere only at considerable intervals, it seems best to calculate all lake saturation standards on the basis of normal lake level pressure.

STANDARDS OF SATURATION

Apparently no one prior to 1929 had questioned the use of the solubility value, with or without correction for altitude, as standard for calculating either " deficits " or percentage saturation. That is to say, if at depth m meters in a lake the temperature be $t°$ C., then the standard of oxygen saturation at that depth would be the quantity of oxygen dissolved in water which is in equilibrium with air at $t°$ C., and either 760 mm. pressure, or the normal air pressure at the lake's surface. Limnologists have not been unaware that the actual pressure at a depth m is much greater than 760 mm. But since only at the surface can water come in contact and be in gaseous equilibrium

with the air, then, quoting Thienemann ('28) "mehr O_2, als im Fruhjahr, zur Zeit der Vollzirkulation, im Oberflächenwasser des Sees vorhanden ist, kann also auch nicht in der Seetiefe auftreten." It is, however, true that at moderate depths this value can be greatly exceeded, owing to the photosynthetic activity of green plants.

In 1929, and more fully in 1930, Alsterberg proposed a new standard of saturation, or "primary constant." This is the solubility of atmospheric oxygen at the normal pressure at the lake's surface and at 4° C. This standard is to be used at all depths below the epilimnion of a lake, in summer, regardless of what temperature may actually prevail there. Alsterberg points out that the last time this water was in contact with the atmosphere was during the vernal circulation, when a temperature of 4° C. prevailed throughout the lake, and that hence all subsequent departure from this 4° C. saturation value can be laid to biological processes. He vigorously contests the claim of Birge and Juday ('14, '21) that all or most of the increase in hypolimnial temperature above 4° C. in summer is owing to mixture with epilimnial water, and maintains rather that it is practically all the result of direct insolation. Penetration of epilimnial water into the layers below, he says, can occur only near the shore of a lake, and only after the epilimnial water is first cooled to a temperature less than that of the water with which it is mixed. In most lakes this is a negligible process. He supports his conclusion by a consideration of the free nitrogen dissolved in lake water, and by observations on the Bodensee, whose surface is almost free from wind disturbance.

The difference between the actual oxygen content in this region and the 4° saturation value is called by Alsterberg the "*absolute oxygen deficit*," as opposed to the *actual* oxygen deficit as used by previous workers. He does not propose that the 4° C. saturation value be used as a primary constant in the epilimnion; in this layer the *actual* oxygen deficit is the best one, since throughout the summer this water is from time to time in contact with the atmosphere. Similarly, for the duration of the vernal and autumnal overturn, the actual saturation values may be used throughout the lake. In winter, under ice, he claims that the saturation value at 0° C. is the best standard, to judge again by the nitrogen values; this point would seem to need further elucidation.

Although Alsterberg's contentions on the whole seem well supported, we need not suppose that immediately the surface water of a lake exceeds 4° C. in spring, all downward circulation automatically stops. While 4° C. is the point of maximum density, yet density changes only very slowly for a degree or so on either side of that point, so that a rise of temperature of one or two degrees C. in the surface water might not constitute an effective barrier to wind-assisted circulation, even to quite a depth. It is well known that winter temperatures at the bottom of even deep lakes fall below 4° C., for example, the Finger lakes of New York, in Birge and Juday ('14). Since the thermal conductivity of water is so poor, this phenomenon affords concrete evidence

that wind-impelled circulation can transport *lighter* water *downward.* Extensive and as yet unpublished temperature series taken in Cultus lake, British Columbia, demonstrate that this process can also occur above 4° C., in spring, and that complete circulation may not cease until the lake is at a temperature of 5° C. or thereabouts, varying with the climatic conditions prevailing each season.

If on any lake a series of oxygen determinations be made at this critical time, just as complete circulation stops, it can be used to calculate a primary constant for that lake for that season. Failing such a series, Alsterberg's 4° constant is the best approximation.

Following closely on Alsterberg's innovation, Maucha ('31, '32) proposes quite a different saturation standard. Thienemann notwithstanding, Maucha is of the opinion that hydrostatic pressure must have a place in such calculations. For, he argues, the consumption of oxygen which proceeds in the tropholytic region of a lake is a " negative production "; and in the lower part of the trophogenic region, water has sometimes been found of such oxygen content that it could exist in equilibrium with air only under twice the normal pressure.

For his solubilities, Maucha used the absorption coefficients as given by Winkler, and subtracts the partial pressure of aqueous vapor in the calculations. He builds up formulae which end in these quantities:

$$g = \frac{O_2}{O_2^1} \cdot \frac{b + m\pi - 760}{b + m\pi - f} \cdot 100,$$

$$g^1 = \frac{b - f}{760 - f} \cdot \frac{b + m\pi - 760}{b + m\pi - f} \cdot 100,$$

where O_2 is the actual oxygen content of the water at depth m meters in a lake,

O_2^1 is the solubility of atmospheric oxygen at temperature $t°$ C., which prevails at this depth, and at 760 mm. pressure, exclusive of aqueous vapor,

b is the normal atmospheric pressure at the surface of the lake, in mm.,

π is the hydrostatic pressure of 1 meter of water, = 73.5 mm.,

f is the partial pressure in mm. of aqueous vapor in a saturated atmosphere at $t°$ C.,

g he calls a " Gradient der Sättigung," which has been translated into " oxygen gradient," but which might more properly be anglicized as a " measure of saturation." It may be described thus: The measure of saturation, g, at depth m meters in a lake is equal to 100, divided by the solubility of oxygen from an atmosphere of pressure 760 mm. and the temperature $t°$ prevailing at that depth, and multiplied

by the difference between the actual oxygen content and the oxygen content which water at the same temperature and of the same percentage saturation[3] (not neglecting hydrostatic pressure) would have, if it were at a pressure of 760 mm.,

g^1 is the measure of saturation, if the actual oxygen content at depth m were to be equal to the solubility of oxygen from an atmosphere at the prevailing temperature $t°$ and the normal air pressure b at the elevation of the lake. It is used as a standard of saturation.

When plotted, values of g^1 increase with depth, but not in a linear progression. Apart from Maucha's own work, values of g and g^1 have been calculated by Juday and Birge ('32) for several Wisconsin lakes.

To the author it appears that Maucha has made a notable but unsuccessful attempt to speak in absolute physico-chemical language in expressing oxygen saturation. After building up his complicated measure of saturation, and equally complicated saturation standard with which it may be compared, in both of which hydrostatic pressure occupies a prominent place, we find that in the process of comparing them (*i.e.*, dividing one by the other) all terms involving hydrostatic pressure disappear, thus:

$$\frac{g}{g^1} = \frac{O_2}{O_2^1} \cdot \frac{760 - f}{b - f}.$$

What is left is merely the percentage saturation of the earlier investigators, corrected for lake elevation.

Maucha used $\Sigma g/\Sigma g^1 . 100$ values below the epilimnion as a measure of oxygen deficit, and hence of the trophic character of lakes. More reasonable would be $\Sigma(g/g^1)/n . 100$, if n is the number of observations used, and this would be merely the average percentage saturation. In the case of all lakes which he records, $\Sigma g/\ g^1$ and $\Sigma(g/g^1)/n$ are nearly the same; the last commonly exceeds the first by 2 to 5 per cent.

Absolute Standard of Saturation

It will be interesting to see how it is possible to give hydrostatic pressure a place in such comparisons, and so to construct a standard of *absolute oxygen saturation*, which may be defined as the oxygen content to which water at a given depth must attain, other physical and chemical characteristics remaining constant, if it is to exist in gaseous equilibrium with an atmosphere, not necessarily of normal composition, at that depth.

Let a volume of water at depth m meters, temperature $t°$ C., and pressure p_m mm. in a lake contain dissolved oxygen, "dissolved atmospheric nitro-

[3] As is shown below, Maucha fails to consider all of the factors which determine "real" saturation at a depth.

gen,"[4] and dissolved carbon dioxide in quantities o, n, c mg./l. respectively. Let q_o, q_n, q_c be the solubility of each gas, *i.e.*, the weight in mg. which will dissolve in 1 liter of water at $t°$ C. from an atmosphere of "pure" gas (*i.e.*, gas + water vapor), when the total pressure is $p_0 = 760$ mm. Now let the quantity of oxygen in this water be increased to the saturation point of x mg. per liter, to the point, that is, where if the water be thoroughly agitated, an atmosphere will begin to be liberated from it. Let the fractions, by volume, of the various gases (except water vapor) in this liberated atmosphere be O, N, C, respectively. $O + N + C = 1$.

Henry's law states that the quantity of a gas dissolved in a liquid is directly proportional to its partial pressure in the atmosphere with which the gas exists in equilibrium. Since partial pressure is proportional to volume, the partial pressure of each gas in this atmosphere is Op_m, Np_m and Cp_m mm. respectively. We may therefore write:

$$x = Op_m . q_0/p_0, \tag{1}$$

$$n = Np_m . q_n/p_0, \tag{2}$$

$$c = Cp_m . q_c/p_0. \tag{3}$$

Solving these three equations, we obtain

$$x = q_0(p_m/p_0 - n/q_n - c/q_c) \text{ .mg./l.}, \tag{4}$$

which is the standard of absolute saturation of oxygen. If any other gas, say methane, were present in the water, it is easy to show that the absolute standard would be further decreased, thus:

$$x = q_0(p_m/p_0 - n/q_n - c/q_c - m/q_m), \tag{5}$$

if m is the quantity of methane present and q_m its solubility.

In most lakes, only oxygen and nitrogen need be considered. Although free carbon dioxide is commonly found dissolved in lake waters, its solubility is so great that quantities up to 50 mg./l. may be ignored, particularly at some depth. In this case, the formula becomes:

$$x = q_0(p_m/760 - n/q_n). \tag{6}$$

As an example, values of x have been calculated in table III, for a series taken in Green lake, Wisconsin, August 20, 1905, by Birge and Juday ('11), using solubilities tabulated in table I. Since titration methods of determining

[4] In what follows, "nitrogen" is taken to mean "atmospheric nitrogen," *i.e.*, 98.815 per cent vol. N_2 + 1.185 per cent vol. A. Both the nitrogen determinations on record and the solubility table quoted, are for this mixture. It would of course be more accurate to consider nitrogen and argon separately. Note that the nitrogen-argon mixture dissolved from "atmospheric" nitrogen contains the two gases in proportion of 97.4 per cent vol. N_2 to 2.6 per cent vol. A. See Maucha ('32, p. 19) for a table of absorption coefficients of argon.

oxygen are now universally employed, it is not easy to obtain nitrogen values such as are used here. If for any reason it is desirable to calculate absolute saturation in such a case, a good approximation may be had by substituting for n in the formula the primary constants of Alsterberg. Compare the last two columns of table III.

TABLE III. *Green lake, Wisconsin (SE. part) 20.VIII.05. Observed data from Birge and Juday ('11), p. 148. Elevation = 275 m. Normal air pressure ($t = 23°$): 736 mm. Sub-epilimnial primary constant, for oxygen 12.7 mg./l., for nitrogen 16.4 cc./l.*

Depth	Total Press.	Temp.	Oxygen				Nitrogen		
			Solub.	Abs. Sat.	Observed quantity	Abs. Sat.	Solub.	Obsv'd quantity	Primary constant
m.	mm.	° C.	q_o.mg./l.	x.mg./l.	mg./l.	per cent	q_n.cc./l.	cc./l.	cc./l.
0	736	23.0	41.5	7.4	8.0	108.	14.7	11.6	11.3
10	1471	20.7	43.3	47.6	5.6	11.8	15.3	12.8	11.7
12	1619	17.3	46.3	61.1	5.7	9.3	16.2	13.1	
15	1838	12.6	51.2	82.5	6.9	8.4	17.7	14.4	16.4
20	2106	8.6	56.0	110.	7.9	7.2	19.3	15.7	16.4
30	2941	7.4	57.6	176.	9.1	5.2	19.7	16.1	16.4
40	3676	6.2	59.4	239.	9.4	3.93	20.3	16.8	16.4
50	4411	6.0	59.7	297.	9.0	3.03	20.4	16.7	16.4
60	5146	5.8	60.0	358.	6.3	1.76	20.5	16.6	16.4
65	5511	(5,8)	60.0	386.	2.0	0.52	20.5 .	16.6	16.4
70	5881	5.7	60.2	418.	0.94	0.22	20.5	16.4	16.4

The distinctive feature of oxygen deficits or percentage saturation values calculated from this standard is the fact that they show to what extent the observed amount of oxygen would need to be changed before there would be any tendency for gas to come out of solution. Consideration of these saturation figures reveals that there is little likelihood of absolute supersaturation occurring anywhere in a lake, except rarely at depths less than five meters.

NORMAL RESPIRATORY VALUE

F. Ruttner, in Brehm and Ruttner ('26), has suggested a novel calculation applicable to oxygen determinations. Because the respiratory rate of aquatic organisms increases with increasing temperature, a quantity of oxygen sufficient for respiration in cool water may be inadequate in warmer water. To take into account this variability in oxygen demand of the biota, Ruttner chooses an arbitrary *normal respiratory value* of 10 milligrams per liter at 15° Centigrade, this being reckoned as 100 per cent. Following Van't Hoff's law, that the speed of a chemical reaction is doubled with each increase in temperature of 10° C., the respiratory value of 10 mg./l. at any other temperature may be found from the formula:

$$\log y = 2.4515 - 0.03010\,x$$

where y is the respiratory value of 10 mg./l. oxygen at temperature x de-

grees C., expressed as a percentage of the normal value. Morton ('31) illustrates this relationship graphically.

Example: At a certain depth in a lake the temperature is 7.4° C., the oxygen content 12.4 mg./1. What is the respiratory value? From the formula or the graph, the respiratory value of 10 mg./1. at 7.4° C. is 169 per cent. The respiratory value of 12.4 mg./1. is therefore $(12.4/10) \times 169 = 210$ per cent.

The weakness of this method of estimation lies of course in the fact that it has not been demonstrated that the respiratory rates of aquatic organisms always or even usually conform closely to Van't Hoff's law. None the less it is an interesting attempt to picture quantitatively the immediate relationship between dissolved oxygen and the creatures which consume it.

Summary

1. A number of chemists have made observations upon the quantity of oxygen which will be dissolved in pure water in equilibrium with the atmosphere at various temperatures and 760 mm. pressure. Tables calculated therefrom may be for 760 mm. *total* pressure, or for 760 mm. pressure, exclusive of water vapor. Care must be taken to distinguish the two kinds. The solubility table of Fox, as calculated by Whipple and Whipple, is probably best for limnological work.

2. The uncertainty in calculation of standard oxygen values which arises from differences in the various sets of observations, may be partially obviated by standardizing analytical reagents by reference to a solubility table.

3. It is desirable that saturation values be calculated to the normal pressure over the lake to which they are applied.

4. There are five different standard oxygen values which have been or may be used in calculating oxygen deficits or percentage saturations. These are:

(*a*) The solubility of oxygen in water from the atmosphere at 760 mm. pressure and the temperature of the water sample under consideration.

(*b*) The solubility of oxygen in water from the atmosphere, at normal lake-level pressure and the temperature of the water sample.

(*c*) The primary constants of Alsterberg:

For summer sub-epilimnion: the solubility of oxygen from the atmosphere at normal lake-level pressure and 4° C.,

For winter, under ice: the solubility of oxygen from the atmosphere at normal lake-level pressure and 0° C.,

For epilimnion in summer, and for the entire lake at time of vernal and autumnal overturn: the solubility of oxygen in water at normal lake-level pressure and the temperature of the sample under consideration.

(*d*) The saturation standard of Maucha (see text).

(*e*) The absolute standard of saturation, which is a function of tempera-

ture, total pressure, and the quantities of gases other than oxygen which are in the water.

Each of these values has its own adherents, and its own field of usefulness, which depends, not only upon what end may be in view, but also upon how much labor it is desirable to expend in arriving at it. From a biological point of view, the primary constants of Alsterberg are as useful and as easy to calculate as any of those given. From a strictly physico-chemical standpoint, the absolute standard of saturation is the one which comes closest to being an expression of the real relationship of oxygen content to prevailing conditions.

5. *Respiratory values*, as calculated by Ruttner, make it possible to compare the availability of oxygen to living organisms in waters of different temperatures.

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THE INFLUENCE OF EXPOSURE TO WINTER TEMPERATURES UPON SEED GERMINATION IN VARIOUS NATIVE AMERICAN PLANTS[1]

G. E. NICHOLS

Yale University, New Haven, Conn.

It has long been known that the seeds of very many plants germinate best, and some only, after being exposed for a more or less protracted period to near-freezing temperatures, under conditions otherwise favorable to germination. Kinzel in particular ('26 and earlier papers) has studied the behavior of a large number of European species in this respect, while similar investigations have been carried on in this country by Rose ('19), Coville ('20), Adams ('27), Crocker ('30), and others. In the main, however, these American investigations have been undertaken from the physiological point of view or from that of the nurseryman and, with the exception of the paper by Adams, the number of native species which have been worked with is very small.

In view of this latter fact, and since information of this sort may possess considerable ecological value, it has seemed worth while to investigate the influence which exposure to winter temperatures has upon seed germination in a considerable number of native American plants. More especially the investigation was undertaken with a view to finding out whether there was any marked correlation between germination behavior in this respect and the geographical distribution of the plants concerned.

MATERIALS AND METHODS

Altogether, in the course of the four years (1927–1931) over which observations were conducted, more than 200 species were experimented with, many of these in two or three successive series. Seeds were collected, mostly by the writer, in various more or less widely separated and ecologically dissimilar localities (see list given below). Following its collection, all material was air-dried, and the seeds of fleshy fruits were usually, although not always, removed from the pulp. For experimental purposes, late in autumn the seeds were counted out in duplicate lots of mostly 100 or 200 each; or else, in the case of very tiny seeds difficult to count, they were measured out in duplicate lots of practically equal size by means of a specially made small glass measuring thimble. They were then planted in sterilized soil, in separate boxes made

[1] Contribution from the Osborn Botanical Laboratory and the University of Michigan Biological Station.

for the purpose. One box of each pair was placed out of doors in a cold frame for a refrigeration period of from 71 to 112 days (or, in one instance, 57 days), while the other box was kept in the greenhouse. In the indoor series, seedling counts were made at intervals of approximately a week for the first two months, and less frequently thereafter. The same procedure was followed with the outdoor boxes, when these latter were brought into the greenhouse at the expiration of the refrigeration period. Observations on individual seed series were continued in some cases for nearly a year and a half, all boxes being kept indoors during the second winter.

Observations and Discussion

Out of the mass of data accumulated in this way, the more essential facts are here presented in tabular form. Five groups of plants (tables I–V) have

Table I. *Seeds germinating only after a period of exposure to low temperatures*

	Number of seeds used	Number of seeds germinating	Number of days required for germination
Aconitum uncinatum (G)	100	34	(71) 21–35
Aralia nudicaulis (M)	100	24	(83) 246–395
Campanula rotundifolia, alpine form (A)	+	+	(71) 14–21
Caltha palustris (M)	100	5	(112) 35–48
Chiogenes hispidula (W)	+	147	(83) 35–98
Circaea alpina (M)	300	141	(83) 28–98
Clintonia borealis (M)	100	1	(83) 445
Cornus canadensis (C)	1000	109	(83) 35–150
Diapensia lapponica (A)	+	+	(83) 21–28
Eupatorium purpureum (S)	200	18	(71) 21–28
Euphrasia americana (C)	+	50	(71) 14–21
Gentiana andrewsii (S)	200	98	(83) 21–84
Iris prismatica (B)	100	45	(83) 21–35
Kalmia polifolia (M)	+	+	(71) 63 194
Lachnanthes tinctoria (B)	200	28	(71) 77
Lonicera oblongifolia (M)	100	9	(83) 21–70
Mikania scandens (G)	200	153	(71) 14–42
Polygonella articulata (M)	100	11	(83) 11–21
Pedicularis canadensis (M)	+	2	(112) 35–44
Pyrus americana (C)	100	9	(83) 25–49
Ribes prostratum (A)	100	26	(83) 21–49
Silene pennsylvanica (S)	200	55	(71) 14–21
Verbena stricta (Kansas)	200	109	(71) 14–63

been distinguished on a basis of the difference in the total number of seeds germinating in the refrigerated and non-refrigerated cultures respectively, as follows: (I) Seeds germinating only after a more or less protracted period of exposure to low temperatures; (II) Germination markedly higher (ratio 5:1 or more) in seeds exposed to low temperatures; (III) Germination distinctly higher (ratio greater than 2:1 but less than 5:1) in seeds exposed to low temperatures; (IV) Germination but little different (ratio between 2:1 and 1:2 inclusive) in refrigerated and unrefrigerated seeds; (V) Germination distinctly lower in refrigerated than in unrefrigerated seeds (ratio less than 1:2).

For the seeds listed in each table, the following data are presented in order: (1) Number, or quantity, of seeds used in each lot; (2) Number, or quantity, of seeds germinating (*a*) after refrigeration and (*b*) without refrigeration; (3) Number of days required for germination, both the number up to the time when first seedlings appeared and the number up to the time when last

TABLE II. *Germination markedly higher (ratio 5 : 1 or more) in seeds exposed to low temperatures*

	Number of seeds used	Number of seeds germinating		Number of days required for germination	
		After refrig.	Without refrig.	After refrig.	Without refrig.
Alnus crispa (A)	200	80	5	(71) 14-35	106-134
Alnus incana (S)	200	23	3	(112) 14-55	126
Alnus mollis (C)	200	71	4	(71) 14-35	76-153
Aletris farinosa (B)	+	+	±	(83) 35	252
Arenaria groenlandica (A)	+	+	±	(71) 14 35	13-69
Betula glandulosa var. *rotundifolia* (A)	200	49	7	(83) 14-28	27-299
Betula papyrifera (M)	200	73	16	(83) 21-56	27-252
Cassiope hypnoides (A)	+	+	±	(83) 21-28	78
Eupatorium rotundifolium (B)	200	12	2	(71) 28-42	106
Iris versicolor (S)	100	26	5	(71) 21 42	106-265
Kalmia angustifolia (B)	+	+	±	(83) 21 28	111-125
Kalmia latifolia (S)	+	+	±	(83) 42	125
Ledum groenlandicum (W)	+	+	±	(83) 21-28	97-111
Leiophyllum buxifolium (B)	+	+	±	(83) 98	252-298
Liatris graminifolia (B)	200	18	1	(83) 20-56	97
Loiseleuria procumbens (A)	+	+	±	(83) 21-28	97
Polygala polygama (M)					
Cleistogamous seeds	100	28	1	(83) 28-70	129
Non-cleistogamous seeds	100	17	3	(83) 21-49	90
Potentilla tridentata (A)	200	147	25	(71) 7-14	78-148
Prenanthes trifoliata, alpine form (A)	100	28	5	(83) 11 56	20-41
Prunus pumila (M)	45	8	1	(83) 21-35	420
Rhododendron canadense (C)	+	+	±	(83) 35	125
Rhododendron lapponicum (A)	+	+	±	(83) 21-28	83
Ribes cynosbati (M)	100	45	8	(83) 21-49	20-252
Sambucus canadensis (C)	100	57	5	(83) 25-70	55-330
Smilacina racemosa (M)	100	30	2	(112)264	376
Smilacina stellata (M)	100	50	7	(71)194-500	148-265
Solidago odora (S)	200	49	8	(83) 21-70	70-97
Tanacetum huronense (M)	200	118	24	(71) 7-42	64-92
Vaccinium uliginosum (A)	200	110	9	(83) 21-70	153-181
Vaccinium vitis-idaea (A, C)	400	147	12	(83) 28-169	252-299

seedlings were observed (*a*) after refrigeration and (*b*) without refrigeration. Also, preceding the figures for germination period in column 3*a*, in parenthesis is given the length of the refrigeration period (in days). The plus (+) sign in column 1 indicates that measured quantities and not counted lots of seed were used. The same symbol in columns 2*a* and 2*b* should be interpreted to mean "considerable germination"; the symbol "±" to mean

"more or less germination." In addition, the geographical source of seed is indicated in each case by a letter in parenthesis immediately following the species name, as follows: southern New England, wild (S); cultivated in Yale Botanical Garden (G); pine barrens of southern New Jersey (B); Maine coast, in vicinity of Penobscot Bay (C); lower slopes (W) and alpine summits (A) of White Mountains, New Hampshire; northern Michigan (M), in general vicinity of the University of Michigan Biological Station at Douglas Lake, Cheboygan County. Unless otherwise designated, the species names are those of Gray's Manual, seventh edition.

As had been anticipated, difficulty was experienced with many seeds in

TABLE III. *Germination distinctly higher (ratio greater than 2 : 1, but less than 5 : 1) in seeds exposed to low temperatures*

	Number of seeds used	Number of seeds germinating		Number of days required for germination	
		After refrig.	Without refrig.	After refrig.	Without refrig.
Aralia hispida (M)	100	8	3	(83) 98-400	125-181
Cornus amomum (S)	200	19	6	(83) 25-35	55-111
Draba arabisans (M)	+	467	106	(83) 11-49	13-48
Fragaria virginiana (M)	200	143	52	(83) 21-56	27-252
Gentiana crinita (S)	200	59	23	(83) 21-28	27-69
Ilex glabra (B)	100	12	3	(83) 277-395	252-511
Maianthemum canadense (M)	100	51	26	(83) 42-84	181-252
Nyssa sylvatica (S)	100	55	27	(71) 28-120	106-265
Pieris mariana (B)	+	208	48	(83) 21	48-111
Ranunculus septentrionalis (M)	200	87	34	(83) 21-49	55-90
Ribes hudsonianus (M)	100	65	25	(83) 21-49	20-167
Sabatia dodecandra (B)	+	170	78	(83) 25-49	48-69
Solidago cutleri (A)	200	151	67	(83) 11-70	20-167
Vaccinium caespitosum (A)	200	66	18	(83) 28-169	83-252
Vaccinium pennsylvanicum (M)	200	103	42	(83) 28-169	48-139
Vaccinium pennsylvanicum var. *nigrum* (M)	200	61	21	(83) 35-169	48-252

securing adequate germination, under the conditions of the experiment, and in a considerable number of cases there was no germination at all. It has not seemed worth while to list these latter. Failure to germinate in some instances was manifestly due to immaturity or infertility of material at the time of collection; in others to the short viability of the seeds or to their inability to survive dessication; in others to the great length of time required for after-ripening. In still others the causes remain to be determined. Brief reference may be made to a few suggestive examples. (1) Seeds of *Dirca palustris,* ripening in June and demonstrated by cutting to be fertile, were planted immediately. At the end of three months there had been no germination, yet all that remained was the empty seed coats. (2) Seeds of *Prunus pennsylvanica* treated in the usual way showed no germination whatever at the end of 17 months in either refrigerated or non-refrigerated boxes, although the

embryos were still sound. It was suggested that this might be one of those seeds which normally germinate only after passing through the digestive tract of some bird; but experiment failed to confirm this idea. Two hundred seeds from cherries which had been eaten and ejected by a captive cedar waxwing or " cherry bird " were planted in two lots, one refrigerated and the other not. Only four of these germinated. On the other hand, 200 seeds in which the bony outer seed coats had been clipped off at one end, so as to expose the

TABLE IV. *Germination but little different (ratio between 2 : 1 and 1 : 2 inclusive) in refrigerated and unrefrigerated seeds*

	Number of seeds used	Number of seeds germinating		Number of days required for germination	
		After refrig.	Without refrig.	After refrig.	Without refrig.
Anemone canadensis (M)	200	34	29	(71) 35–49	64–78
Anemone cylindrica (M)	100	10	9	(83) 169–308	90–330
Anemone multifida (M)	200	86	80	(83) 21–49	27–90
Aquilegia canadensis (M)	400	339	234	(83) 21–56	27–90
Antennaria neodioica (M)	+	+	+	(83) 11–21	13–90
Arisaema triphyllum (S)	100	79	82	(71) 21–63	34–92
Arnica mollis (A)	200	3	5	(83) 28	20
Asclepias tuberosa (G)	100	90	46	(71) 21–49	34–134
Aster novae-angliae (G)	200	129	123	(71) 14–28	43–78
Baptisia tinctoria (S)	70	54	69	(112) 14 217	51–329
Campanula rotundifolia (M)	+	+	+	(83) 11–28	13–69
Cassia chamaecrista (B)	100	20	18	(71) 14–77	15–148
Cercis canadensis (Tenn.)	100	2	1	(83) 25	167–181
Chrysopsis mariana (B)	200	80	44	(83) 11–70	41–90
Cirsium hillii (M)	50	36	26	(83) 11–98	13 41
Cirsium muticum (S)	200	16	16	(83) 21–42	29–299
Cirsium pitcheri (M)	200	169	97	(71) 7–28	13–69
Coreopsis lanceolata (M)	100	62	90	(112) 14–217	90–329
Cornus circinata (M)	100	26	45	(83) 98–654	83–520
Cornus stolonifera (M)	100	25	14	(83) 21–277	252–510
Corydalis glauca (S)	100	47	45	(83) 21–42	20–21
Elymus arenarius (C)	100	78	51	(83) 11–28	13–69
Empetrum nigrum (A)	100	3	2	(83) 169	299
Epilobium angustifolium (C)	+	938	658	(83) 11	13
Fragaria vesca (M)	200	91	64	(83) 14–56	48–252
Gentiana porphyrio (B)	+	100	50	(71) 14–21	43
Geum peckii (A)	300	22	14	(83) 11–42	34–83
Geum rivale (M)	300	70	83	(83) 14–35	20–90
Geum strictum (M)	300	211	152	(83) 11–35	13–41

embryo, gave 35 per cent germination within two weeks after being brought into the greenhouse, and 42 per cent within a month, following 4 months refrigeration out-of-doors; while another lot, similarly clipped but planted in the greenhouse, gave no germination within 6 weeks, at the end of which time only the empty seed coats remained. (3) Seeds of *Taxus canadensis* and *Clintonia borealis* were still sound at the end of 21 months in both refrigerated and unrefrigerated material; but the only sign of germination was a single

Clintonia seedling which had appeared during the seventeenth month. (4) Seeds of *Myrica gale* collected in April, after they had been on the bushes all winter, gave germination results which were very different from those given by seeds collected in August (see table V), as follows:

(*a*) 200 seeds sown on wet filter paper in petri dishes and placed in west window, where exposed to afternoon sunlight, gave 41 per cent germination in 3 weeks and a total of 43 per cent in 5 weeks.

TABLE IV—*continued*

	Number of seeds used	Number of seeds germinating		Number of days required for germination	
		After refrig.	Without refrig.	After refrig.	Without refrig.
Helianthus angustifolius (B)	200	32	24	(71) 21–42	64–106
Houstonia caerulea var. *faxonii* (A)	200	150	157	(71) 28	22–120
Linnaea borealis (M)	200	44	57	(71) 28–49	76–273
Lithospermum gmelini (M)	50	3	4	(83) 25–84	34–139
Lobelia cardinalis (S)	+	366	219	(83) 21–98	27–90
Lonicera canadensis (M)	100	111(!)	98	(83) 35–84	34–90
Lonicera dioica (M)	100	93	93	(83) 42–98	34–111
Lonicera hirsuta (M)	100	43	43	(83) 70–169	41–97
Lophiola aurea (B)	+	±	±	(83) 42–84	90
Lupinus perennis (S)	100	41	41	(71) 7–63	15–106
Mitella nuda (M)	200	125	84	(83) 64–98	48–139
Nemopanthus mucronata (M)	100	14	28	(83) 338–565	252–511
Phyllodoce caerulea (A)	+	+	+	(83) 21–28	83–125
Phytolacca decandra (S)	100	85	61	(71) 21–77	64–265
Rhamnus alnifolia (M)	200	82	78	(83) 28–390	41–474
Ribes tristis (M)	100	69	73	(83) 169–277	41–125
Sarracenia purpurea (B)	200	16	13	(71) 42–49	64–120
Senecio aureus (M)	50	50	46	(83) 11–35	13–41
Senecio balsamitae (M)	200	180	190	(83) 11–98	13–83
Shepherdia canadensis (M)	100	14	14	(83) 11–21	252–511
Solidago macrophylla (W)	100	50	39	(83) 11–21	13–167
Ulmus serotina (Tenn.)	100	46	26	(83) 21–42	90–181
Vaccinium canadense (M)	200	21	22	(83) 35–169	111–252
Vaccinium corymbosum (S)	200	89	106	(83) 49–216	41–252
Vernonia noveboracense (S)	100	78	57	(83) 11–21	34–90
Viburnum nudum (B)	100	58	72	(71) 63–194	92–148
Viburnum opulus var. *americanum* (W)	100	71	72	(112) 62–217	153–329

(*b*) 200 seeds sown as above but placed in dark cupboard showed no germination at the end of 3 weeks; and thereafter only 11 per cent during the 6 weeks following their transfer to a position alongside *a*.

(*c*) 200 seeds sown as above but refrigerated for 4 weeks at 5° C. gave 54 per cent germination within 3 weeks after being placed alongside *a*, with a total of 58 per cent in 5 weeks.

(*d*) 300 seeds sown on moist earth in glass-covered pot and place outside north window gave 29 per cent germination in 3 weeks and a total of 40 per cent in 6 weeks.

(*e*) 300 seeds treated as in *d* and placed alongside, but covered with blackened glass, gave a germination of only 1 per cent in 3½ weeks and none thereafter during a total period of 8 weeks.

Considered as a factor of ecological importance in relation to the northward geographical distribution of plants, it is obvious that there are two ways in which seed exposure to low winter temperatures may influence germination behavior in the plants concerned. It may influence the proportion of fertile seeds which will germinate, resulting in either an increased or decreased number of seedlings, as compared with seeds not so exposed; it may influence the length of the germination period, both the number of days before germination begins and the length of time over which germination, once started, continues. The first effect is the one with reference to which the plants studied have been grouped in tables I–V; but the second effect may be equally important. As will be seen from examination of the tables, exposure to low winter temperatures ordinarily results in a shortening of the germination period, which in many cases is very pronounced. Such an effect may be of great ecological importance to plants of northward distribution, since it enables them to make the most of a relatively short growing season. The behavior of *Shepherdia canadensis* (table IV) in this respect is particularly striking. In this plant no difference whatever was found in the number of seeds germinating, but there was a remarkable difference in the length of the germination period in the two cultures, namely 11–21 days for refrigerated seeds as compared with 251–511 days for seeds which had not been so treated.

TABLE V. *Germination distinctly lower in seeds which have been exposed to low temperatures (less than 1 : 2)*

	Number of seeds used	Number of seeds germinating		Number of days required for germination	
		After refrig.	Without refrig.	After refrig.	Without refrig.
Alnus rugosa (S)	200	26	62	(83) 25–70	48–111
Arenaria stricta (M)	+	1	14	(83) 185	13–83
Eryngium aquaticum (B)	200	10	76	(71) 42–49	27–90
Gaylussacia baccata (M)	200	13	44	(83) 42–169	111–330
Gaylussacia frondosa (B)	200	3	13	(83) 169–550	125–511
Lathyrus maritimus (M)	100	3	8	(83) 21–84	13–27
Magnolia grandiflora L. (Tenn.)	100	0	35	—	90
Magnolia virginiana (B)	100	3	15	(83) 169–440	78–420
Mitella diphylla (M)	200	37	134	(83) 35–98	41–69
Myrica carolinensis (S)	100	2	13	(71) 77	106 148
Myrica gale (M)	100	1	11	(83) 247	83–330
Rubus idaeus var. *canadensis* (M)	100	26	60	(83) 98–169	90–390
Sambucus racemosa (M)	100	11	51	(83) 70–169	139–252
Trientalis americana (M)	200	0	73	—	111–181
Viburnum alnifolium (W)	100	26	60	(83) 84–307	69–330
Viburnum cassinoides (M)	100	6	23	(112) 70–217	207–376
Viburnum dentatum (S)	100	8	65	(83) 397–427	391–511

Crocker has shown, for a considerable number of plants which are important in nursery practise, that there is not only a "best temperature" at which different seeds should be stratified previous to germination, but also a "best time" for which this treatment should be continued. With regard to the behavior of native wild plants in this respect, the present experiments are not conclusive. Evidence in favor of a "best time" is suggested by the germination behavior of 18 species which were refrigerated in duplicate lots for 71 and 83 days respectively. In 44 per cent of these cases the seeds exposed to the shorter refrigeration period germinated more quickly and in 39 per cent, those exposed to the longer period; but in 17 per cent there was no difference. Corresponding figures for 16 species in which the seeds were refrigerated for 83 and 112 days, respectively, were 25, 44 and 31 per cent; for 4 species refrigerated 71 and 112 days, they were 25, 25 and 50 per cent. The germination behavior in *Cornus canadensis* is even less conclusive.

Seeds	refrigerated	57	days	germinated	11	per	cent	in	68–82 days
"	"	83	"	"	4	"	"	"	35–42 "
Fruits	"	57	"	"	23	"	"	"	61–96 "
"	"	83	"	"	5	"	"	"	150 "
"	"	112	"	"	10	"	"	"	35–83 "

In comparing rapidity of seed germination as affected by length of preliminary exposure to cold, the fact may be significant that, with all three of the refrigeration periods used, the subsequent germination period was essentially identical. Thus the average number of days which elapsed between the time cultures were brought into greenhouse and the appearance of first seedlings was 21 for 46 species which had been refrigerated 71 days and 22 both for 82 species which had been refrigerated 83 days and for 20 species which had been refrigerated 112 days. These figures are for species in which germination started in less than 50 days and are of known application only within the refrigeration limits here employed.

Incidentally, among the numerous features of detailed behavior which were noted among the various individual species dealt with, there is one which stands out as being of unusual interest. Two sets of *Campanula rotundifolia* seeds were collected, the first in 1928 from normal vigorous plants, a foot or more in height, growing among the sand dunes along the Straits of Mackinac in northern Michigan; the second in 1929 from dwarf alpine plants, less than 6 inches high, growing above timber line, at an elevation of about 5000 feet, in the White Mountains. The station for the latter, situated a short distance east of the Appalachian Mountain Club "Lake of the Clouds Hut," in all probability is the same "stony alpine moor on Mount Monroe" from which Tuckerman (1843) described his "variety *alpina*" of this species. Seeds from the lowland plants germinated abundantly in both refrigerated and unrefrigerated cultures, in the ratio of about 5 to 3; while seeds from the alpine

plants germinated abundantly in the refrigerated culture but not at all in the other. But this is not all. Seedlings of both forms were transplanted to outdoor conditions in the Yale Botanical Garden, where they have now been growing side by side, under ordinary garden conditions, for three years. The offspring of the lowland plants, as was expected, resemble their progenitors; but so also do the offspring of the alpine forms which for three summers now, while occasionally sending up a somewhat taller shoot, on the whole have maintained the dwarf habit of their parents.

Examination of the tables reveals puzzling discrepencies in the germination behavior of a number of species. How far these represent the effect of differences in environment and how far they are due to chance or to faulty technique is a question which must be left for future investigations to decide. By and large, among those plants of northward distribution which were studied there can be no question as to the advantageous influence of winter refrigeration in stimulating seed germination, while a similar relation seems to hold for many plants of southward distribution. A more extended study of some few carefully selected examples of both northern and southern plants with reference, among other things, to optimum refrigeration temperatures and times, would be well worth while. To others who may contemplate such studies it is suggested that the petri dish method, as used by Kinzel and others, is distinctly preferable to the soil culture method used by the writer; that results will be more conclusive if much larger numbers of seeds are employed; that presence and absence of light should be taken into account as possible determining factors; that provision should be made for continuing observations, when necessary, over a period of several years.

Summary

1. The influence upon seed germination of exposure to winter temperatures was studied in a large number of native eastern American plants, mostly species of northward distribution.

2. Tables are presented showing the germination behavior of seeds in 141 species, both after exposure and when not exposed, figures being given in each case for number of seeds used, number of seeds germinating, and number of days required for germination.

3. The conclusion is reached that winter refrigeration of seeds, in its effect both upon the number germinating and upon the length of the germination period, may be an ecological factor of much importance in relation to the northward distribution of plants.

4. Attention is called to the persistence of the dwarf habit of their parents in plants of *Campanula rotundifolia* which were grown from seed produced by the alpine form of this species, growing on Mount Monroe, in the White Mountains.

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SIGNIFICANCE OF EXTREME OR INTERMITTENT CONDITIONS IN DISTRIBUTION OF SPECIES AND MANAGEMENT OF NATURAL RESOURCES, WITH A RESTATEMENT OF LIEBIG'S LAW OF MINIMUM[1]

WALTER P. TAYLOR

Biological Survey, U. S. Dept. of Agriculture

Action of the environment on the organism or the biotic community is not uniform or consistent. Unusual features are quite "normal." Extreme conditions are probably more significant in appraising action of environment than are the more ordinary environmental relationships.

Extremes of greatest importance are those of temperature (heat or cold), moisture (drouth or flood), and wind, although effective extremes might develop in any other fluctuating environmental factor. The whole subject needs further study. As Patton ('30) says, species are not adapted to average conditions, but to the exceedingly unfavorable conditions experienced from time to time.

EXTREMES IN ARID AREAS

In a desert or semi-desert region almost every environmental relationship is colored by the effects of extreme years. In such regions it is usually the hottest, driest year that exercises the most far-reaching influence on vegetation and animal life. The more severe the season, the greater its importance from the distributional and ecologic standpoints. In a drouth year overgrazing by livestock, game species, and rodents is much more likely to occur than under average conditions. Grasses and other plants are killed on the desiccated lower slopes and restricted to the somewhat less dry slopes above. The effects of these extreme seasons can sometimes be seen at the margins of types, particularly along lines between grassland and barren, desert areas or on boundaries between forested and nonforested tracts.

Occasionally, sometimes regularly, the effects of extreme seasons are recorded far away, both in distance and in time, from the regions of their original incidence. Thus in desert or semi-desert areas the extremest and severest effects on vegetation are registered in the driest years, as just stated, but some of the most serious end-results of these dry-year effects are not recorded until several years later. Superabundant rainfall on the arid lands, often in the form of cloudbursts, unimpeded by soil-protecting vegetation,

[1] I am indebted to C. K. Cooperrider, Southwestern Forest and Range Experiment Station, for reading this paper and making valuable suggestions.

results in abnormal erosion wherever water has an opportunity to cut into the surface, and disastrous floods and deposition of debris on the lower courses of rivers take place, perhaps many miles from the scene of the original dry year effects.

It is common knowledge among those living in arid or semi-arid lands that the occasional torrential flood will do far more to erode the landscape and change its topography than many periods of normal rainfall. The same is true of the work of the waves on a sea-cliff. The occasional tremendous storm may wear away the seacoast to more than make up for the possible accumulations of sediment in normal years. Bretz ('32) has suggested that the Grand Coulee (the origin of which was long a puzzle), in Washington State, through which once ran a stream that plunged over a precipice five times as high as Niagara with a waterfall seven times as wide, was formed by a vast flood due to the sudden bursting of an ice dam during the glacial period. It is probable that in many instances buried ancient ruins and cities were not covered by slow and gradual accumulation of wind-blown or water-carried material over many years, but overwhelmed almost at once with an irresistible quantity of stones, detritus, and silt, as were some of the streets of Montrose, Glendale, and other places near Los Angeles, California, in the tremendous storm of New Year's Day, 1934.

Russell ('32) has made a significant study of the frequency of dry and desert years in the arid climates of the United States. He concludes that there is a distinct possibility that an occasional dry or desert year has greater significance in landscape than do the facts of normal climatic distribution, that in many natural processes an extreme condition, though occupying very little time and occurring infrequently, has far greater significance than have normal conditions. Russell points out (p. 271) that the eastern border of the regions of mesquite and mesquite grass in Texas, and of bluestem bunch grass in Oklahoma and Kansas, is very close to the limits of the region experiencing at least one desert year during the period 1901–1920. The question is raised whether this particular vegetational boundary is not more closely related to the occurrence of an occasional extreme drouth than to the normal climatic boundary. Russell suggests further that it is reasonable to suppose that under normal conditions the oak-hickory and prairie-grassland associations tend to migrate westward into the shorter grassland territory; that where edaphic conditions are favorable such migration actually occurs during normal and more than normally humid years; but that an occasional desert year effectively stamps out the westward progress that goes on during most of the time, and thereby is the chief climatic factor influencing distribution.

Extremes and Geographical Distribution

A number of ecologists have recognized the importance of "abnormal" seasons and years in influencing distribution. Thus Weese suggested ('26)

that studies "should take into account not only averages but critical years, which have a very great influence in delimiting the distribution of species at or near the borders of their range."

Many of our isolated desert ranges in Arizona and New Mexico lack the wild turkeys that are such valuable and interesting features of the fauna of the more extensive areas of mountain and plateau in other parts of the region. There is little doubt that seasons and years of critical character are in part (or perhaps wholly in some instances) responsible for the absence of desirable species from particular areas where they used to occur. This is one of the reasons why: "The smaller the disconnected area of a given zone (or distributional area of any other rank), the fewer the types which are persistent therein" (Grinnell and Swarth, '13, p. 385). This principle applies not only to islands, but also to valleys and mountain ranges that are isolated.

In other cases restriction in the geographic range of certain species is forced by extreme seasons. A species of small numbers and limited distribution, as the masked bobwhite (*Colinus ridgwayi*), formerly occurring in southern Arizona, may be wiped out over much of its range in a single unfavorable season. It is probable that complicating factors are almost always present. But extreme drouth, or cold, or other critical feature of the surroundings must often be the immediate factor that results in limitation of the species or even its elimination.

Of course, periods of extremes not only restrict but extend. They restrict those species that are not tolerant of the degree of the factor attained; and they extend the ranges of species that are tolerant. Lippmaa (see Griggs, '30, p. 608) has pointed out that while fog and cloudiness are very prevalent in the Arctic, prolonged periods of clear, hot weather occasionally occur. Lippmaa thinks that these are critical factors determining survival among Arctic plants. The rare frosts in subtropical countries are believed to exercise a similar influence.

Thus while climatic extremes must drive out certain species or cause them to migrate from a region, they must often permit invasion and establishment of others. In this way extremes, and especially intermittent or irregular extremes, must exercise a very potent influence indeed on the composition of many a biotic community.

An unusually good example both of restriction and of extension is afforded by the ice age. As the ice advanced, carrying with it a colder climate than had previously prevailed in and near the covered area, the great ice-mass with its associated climatic extremes restricted the ranges of warm-adapted, and extended those of cold-adapted, species.

Environmental Extremes and Evolution

Extreme, intermittent, and unusual expressions of environmental factors may play a part in stimulating variation and organic evolution. Many biolo-

gists have called attention to the fact that evolution has not always proceeded at a uniform rate, but rather by jerks. At certain periods living matter appears to become far more mobile and active than it was before or than it becomes shortly after. Nobody seems to know the precise relation of irregular environmental extremes to these periods of unusual protoplasmic activity.

Economic Applications

From an economic standpoint it should be obvious that the welfare of a number of valuable resources depends on proper management during years of extreme conditions. The integrity of the range live-stock business, for example, depends on the success of plans to tide over years of unusual drouth or of abnormal cold and deep snow.[2] The welfare of the valuable vegetation and animal life of a farm, forest, or range area depends on the manager's ability so to protect his crops that extreme cold or drouth will not be disastrous. There is no justification for extensive development of citrus groves or other crops in areas where severe frosts at intervals, perhaps of several years, will kill the trees—unless, that is, protective measures can be employed successfully, and unless the returns between times will suffice more than to make up for the heavy losses bound to occur on these occasions. Similarly, the maintenance of valuable species of fur-bearers, game, or other wild life will depend on the existence of livable conditions at the period of the most critical character. It is of little permanent value to import Mexican quail into a northern State, to protect them carefully, and to provide wild lands for them, where extremes of winter weather will inevitably kill them.

The effects of hunting for sport during years of extremes, either of heat, cold, drouth, or flood, are likely to be far harder on the native stock of game than at other times. For extremes of climate or weather make the game species less able to escape the hunter, and may interfere with reproduction. Drouth may eliminate certain feeds and cut down the fawn crop in deer. Unusually heavy rainfall during the breeding season is known to reduce the percentage of hatching in the Gambel quail of the southwestern United States.

The fluctuations in abundance of flesh-eaters and herbivores of the northern parts of both North America and Asia appear to be associated with extreme conditions of climate in some way little understood. Extremes of cold drive northern flesh-eating birds, as the Cooper and Sharp-shinned Hawks, Goshawks, and Snowy Owls southward into the range of the Bobwhite Quail and other species of game, which as a result may suffer heavy losses.

Study of the geologic section reveals evidences of intermittent and unusual occurrences of far-reaching significance at intervals through past ages. There is need for a sufficient qualification of the hypothesis of uniformitarianism to care for these cases. One may perhaps risk a Hibernicism and say that

[2] Forsling ('24, p. 5) has already emphasized that in the southwestern United States the number of breeding cattle should be limited to range capacity in poor years.

catastrophic occurrences are important, if not frequent, items in the orderly processes of nature. These occurrences are no less normal than the rest; but in order to recognize their normality, one must take a somewhat more comprehensive view of the world and nature than is ordinarily in evidence.

Unless preparation is made, in the administration of all sorts of biological resources, for extreme conditions of an intermittent character, irreparable damage is almost certain to occur in these unusual cases, and the results of painstaking and careful administration of many years are likely to be lost in a single dramatic, if not tragic, episode.

Restatement of Liebig's Law of Minimum

Liebig's Law of Minimum may be phrased as follows (see Chapman, '31, p. 107): When a multiplicity of factors is present and only one is near the limits of toleration, this one factor will be the controlling one.

The importance of extremes in environmental influences apparently necessitates the restatement of this " law " in somewhat the following fashion: The growth and functioning of an organism is dependent upon the amount of the essential environmental factor presented to it in minimal quantity during the most critical season of the year, or during the most critical year or years of a climatic cycle.

Conclusions

If one must choose, he should apparently study extreme rather than average environmental conditions if he wishes to make the greatest progress in respect to distribution, management, and other enterprises involving biological resources. The ideal situation is to acquire adequate knowledge of both.

Recognition of the importance of extreme conditions, often of an intermittent character, carries with it very definite implications for practice.

(1) Since details of the influence of extreme and intermittent conditions would often be entirely missed in short-period observations or experiments, the desirability is obvious of long-time research projects. Research activities cannot be suspended, even in times of severe depression, without risk of almost complete futility. Incomplete and inconclusive investigations often mean the virtual loss of money previously invested in the studies. There should be added, also, on the debit side, wastes and losses in processes to the improvement of which the results of completed researches would have contributed.

(2) In seasons or years of climatic extremes, more than ordinarily conscientious attention should be given to game protection, grazing by livestock, wild-life relations generally (including the influence of insectivorous birds and rodents, as well as of all other forms of wild life), fire protection, and similar problems. Land-use policies, range administration, forest conservation, and game protection should be adjusted not to average conditions, but to those poorer than average, if not to those that are extreme.

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ARTIFICIAL WATERING OF LAWN GRASS

F. A. Welton, J. C. Carroll, and J. D. Wilson

Ohio Agricultural Experiment Station, Wooster, Ohio

In the spring of 1927 a lawn experiment was started, one of the principal objects of which was to determine the quantity of water required to maintain various grasses in a vigorous condition throughout the growing season. For this part of the experiment, five plots were used, each containing one one-hundredth acre (12 by 36⅓ ft.). The two check plots received rainfall only; the other three received not only the natural precipitation but enough additional water to make the total equivalent to 1.5, 2.0, and 3.0 times the normal, respectively. By " normal " is meant the 36-year average rainfall as determined by the Weather Bureau at Wooster, Ohio. Thus, the plot represented by 1.5 N received a quantity of water which exceeded that which would normally fall on it by 50 per cent, the 2.0 N an excess of 100 per cent, and the 3.0 N an excess of 200 per cent. Since in the years of this test the rainfall during the period of watering was sometimes below normal, the excess received by the artificially-watered plots over the checks was, of course, correspondingly greater than that indicated. On account of differences in early rainfall from year to year, the time at which watering was started varied and was as follows: July 15, 1927; June 8, 1928; July 22, 1929; and May 15, 1930. All the plots were divided into three equal parts, one third of each being devoted to Kentucky blue grass, *Poa pratensis*, one third to Chewing's fescue, *Festuca rubra fallax*, and one third to the Washington strain of creeping bent, *Agrostis palustris*.

Effect of Heavy Watering

The plot to which the smallest quantity of water was added artificially received enough to maintain the grass in a green, growing condition throughout the dry weather of each summer. In one of these years (1930) Ohio suffered one of the severest droughts in its history, the rainfall at Wooster for the months May–October, inclusive, being only 61 per cent of the normal. The appearance of the grass on the check plots was inferior each season during the period of dry weather, and in 1930 it became exceedingly brown and dry. In most of the years included in this experiment, it showed signs of growth earlier in the spring than did the artificially-watered plots.

The grass was cut at irregular intervals, the frequency varying with the growing conditions. The quantity of grass obtained during the artificial

watering periods and expressed in pounds (green weight) per 1000 square feet of plot area was as shown in table I.

TABLE I. *Quantity of grass produced during period of artificial watering*

Year	Green weight—pounds per 1000 sq. ft.			
	Unwatered	1.5 normal	2.0 normal	3.0 normal
1927	115.2	190.0	209.7	202.5
1928	146.8	161.6	165.3	180.0
1929	93.1	166.3	169.0	164.6
1930	37.7	157.8	157.4	184.8
4-yr. av.	98.2	168.9	175.3	183.0

Statistical analysis of the results indicate that the water was responsible for a significant increase in the growth of grass but that the quantities used in excess of 1.5 N were superfluous. Perhaps they were even detrimental since in the following year (1931) all the plots were poorer than the check (one plot only was not watered artificially in 1931) and the greater the quantity of water that had been applied, the poorer was the grass. The check plot remained satisfactory and was the only plot on which the growth was increased in 1931 as compared with that made in 1930, table II.

TABLE II. *Quantity of grass produced during the entire season*

Year	Green weight—pounds per 1000 sq. ft.			
	Unwatered	1.5 normal	2.0 normal	3.0 normal
1927	190.4	291.1	297.7	309.1
1928	228.4	261.9	263.6	270.6
1929	278.7	377.3	359.1	389.8
1930	129.0	253.3	255.0	273.4
1931	211.6	238.9	202.0 [1]	215.0
5-yr. av.	207.6	284.5	293.8 [2]	291.6

[1] 1.25 N in 1931. [2] 4-year average.

On the watered plots a noticeable thinning out of the grass had occurred (1932) and this apparently was a reflection of the root development for, with each added increment of water, there had come to be a decreased quantity of underground growth (roots and rootstocks) as shown in table III. The weights as recorded in the table were estimated from the quantity of subterranean parts found in a volume of soil 5 feet long, 2 inches wide, and 2 inches thick. The root material was carefully washed out of the soil, oven-dried to constant weight at approximately 101° C. and weighed. Since it is impractical to remove the last traces of closely adhering soil particles, the dried samples were then ashed at a low red heat. Assuming that all the adhering material was non-combustible, then the loss by ignition represented the approximate weight of the roots. The weight of ash was disregarded for, as stated by McCall ('16) the relative weights would be affected only by the dif-

ference in weight of ash of the various samples and for practical purposes that may be ignored.

The oven-dry weight averaged approximately 36 per cent higher than that obtained by ignition.

TABLE III. *Quantity of roots and root-stocks of Kentucky blue grass*

	Dry weight—pounds per 1000 sq. ft.			
Soil horizon	Unwatered	1.5 normal	2.0 normal	3.0 normal
1st 2 inches	75.79	56.35	50.63	46.83
2nd 2 "	4.39	3.44	3.39	1.80
3rd 2 "	1.88	1.19	0.82	0.69
4th 2 "	0.98	0.79	0.42	1.85
Total 8 inches	83.04	61 77	55.26	51.17

Indications of a thinning out of the grass in the fescue section. however, were in evidence before 1931. Some clover was coming in, but the most conspicuous intruder was velvet grass, *Notholholcus lanatus* (L.) Nash, as may be seen in figure 1. In the check plots there was practically none of this grass

FIG. 1. Velvet grass gaining a foothold in Chewing's fescue (right).

but in the watered plots there was a high correlation between the quantity of water used and the number and size of the patches of the velvet grass. Undoubtedly the sod webworm was an important contributing factor in the final destruction of the fescue in 1931, for in that year there was an unusually fierce outbreak of this pest which showed a preference for certain fescues and bents. The sod webworm did not interfere seriously with Kentucky blue grass; hence, the failure of this section could not well be attributed to the webworm for other plots of Kentucky blue grass less than 30 feet removed from these came through the summer without apparent injury. An illustra-

tion of the selective habits of the sod webworm for grasses is shown also in figure 2. This is a view across 11 plots in a rate-of-seeding test, the left third of each plot being seeded with a Kentucky blue grass-redtop mixture, the middle third with Chewing's fescue alone, and the right third with a mixture of Kentucky blue grass and Chewing's fescue with the proportion of the latter increasing toward the foreground. On the middle- and right-hand sections,

FIG. 2. Sod webworms showed a preference for Chewing's fescue. Kentucky blue grass-redtop mixture (left) undisturbed; Chewing's fescue (middle) and a mixture of Kentucky blue grass and Chewing's fescue (right). Practically all of fescue had been replaced by weeds.

practically all of the Chewing's fescue had been destroyed and in its stead weeds of many sorts had taken possession.

It is possible that the reaction of the soil may have been a contributing factor in the failure of the Chewing's fescue, for the water used contained considerable lime and changed the reaction of the soil from pH 6.5 to pH 7.1. Other tests indicate that Chewing's fescue may have a preference for soils with a relatively high acidity. The decreased acidity, however, would hardly account for the failure of the Kentucky blue grass.

A New Method of Watering

If excessive watering may be injurious to grass, then it is probable that much injury has been done to many golf greens for, on some of these, water is used in lavish quantities. If, therefore, a means could be devised which would indicate not only when water is needed but also the approximate quantity, the method should be helpful to greenkeepers; it would also be an aid to lawn owners, since excessive artificial watering of lawns is of questionable

value. Unless enough water is added to maintain a thrifty green appearance, the primary purpose for which it was added is largely vitiated. Furthermore, especially during very dry periods, the quantity required to maintain the grass in a good growing condition is often prohibitive on account of cost.

In devising such a method, consideration should be given not only to the rainfall but also to the rate of evaporation which, in turn, is dependent on such factors as sunshine, wind velocity, relative humidity and temperature. This is true since it is not the total water which falls but only that which remains in the soil that governs the growth of the grass. An instrument which largely fulfills the requirements involved and of which use was made in 1931 in artificially watering one of the two check plots is Livingston's ('15) standardized spherical black atmometer. The outcome of this preliminary trial was so promising that the experiment in a modified and enlarged form was repeated in 1932, all of the watering plots, on account of failure in 1931, having been plowed up in the late fall of that year and reestablished in the spring of 1932.

For the purpose of this report, only three of the newly established plots will be considered—a check and two others which were watered on the basis of evaporation increments. These were determined by the use of two black atmometers to which reference has already been made. They were installed in the usual way near the watering plots; one plot was watered as soon as 280 cc. (all atmometer readings represent corrected values) of water had evaporated and the second as soon as 360 cc. had evaporated. In case a rain of 0.5 inch or more occurred before these quantities had evaporated, no water was added artificially but the bottles were refilled with distilled water and the process started over again. At each artificial watering the equivalent of one inch of rainfall was added (623 gallons per 1000 sq. ft.).

From the new seeding a fairly good stand of grass was obtained, but before it became well established it began to suffer from dry weather. Both rates of watering, however, maintained the grass in a green condition through-

Fig. 3. Watered after evaporation of 280 cc. (left) and unwatered. Both seeded April 21, 1932. Photographed July 2, 1932. Drought conditions began to prevail about the middle of May.

out the summer and were sufficient to make the difference between fairly good success on the one hand and almost complete failure on the other, for much of the grass on the unwatered plot perished (fig. 3). In the early part of the season the plot receiving the more liberal supply of water presented the better

appearance, but in the latter part of the year the difference largely disappeared.

The growth behavior of the grass throughout the season corresponds closely with the water-supplying power of the soil as determined by soil points; the results are shown in figure 4. The methods used in determining the water-supplying power (that is, the water absorbed per hour at a depth of 6 centimeters by a soil point with an absorbing area of 12 sq. cm.) were the

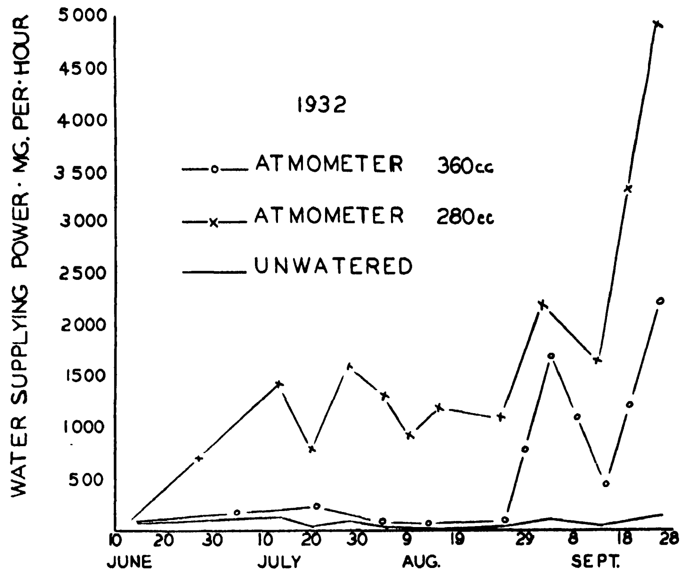

Fig. 4. Growth of grass in relation to water supplying power of soil as measured with soil points.

same as those described by Welton and Wilson ('31). Four soil points were used on each plot for each set of determinations. Thus, the values in each case represent the average of four instruments. The determinations were made at irregular intervals during the months of June, July, August, and September, the dates being regulated by the time of watering. The determinations were usually made the day before watering. The average water-supplying power found was 67 mg. on the unwatered plot, 577 mg. on the plot watered after the evaporation of 360 cc., and 1561 mg. on the one watered after the evaporation of 280 cc. The fact that only the grass on the unwatered plot (with an average water-supplying power of 67 mg.) was severely injured was in agreement with the findings of Wilson ('27) who concluded that 100 mg. was the minimum value below which grasses would be definitely injured through lack of water. Although the plot watered after 360 cc. had evaporated had an average water-supplying power for the season of 577 mg., yet up to September 1 it had a water-supplying power of only 123 mg.; and during that period the appearance of the grass was not all that could be de-

sired. This result also is in agreement with the findings of Wilson ('27) who concluded that a water-supplying power of 500 mg. per soil point per hour at the 6 cm. depth was necessary for good growth of lawn grass.

Since the appearance of the plot watered after the evaporation of 280 cc. was satisfactory throughout the season, its average water-supplying power of 1561 mg. was probably in excess of what was needed.

The summer of 1932 proved to be a good one in which to make such a study as the one herein reported, for the rainfall throughout the season was subnormal. For the months of May, June, July, August, and September, the rainfall was 48.5, 86.2, 76.6, 55.1, and 60.7 per cent, respectively, of the normal.

Cost of Artificial Watering

The quantity of water applied from May 23 to October 1, inclusive, on the plot watered on the 280 cc. basis was 4320 gallons and on the 360 cc. basis, 2700 gallons. Since the condition of the plot receiving the lesser quantity was not altogether satisfactory in the early part of the season and since the one receiving the larger quantity evidently received all and perhaps more than was needed, it is probably fair to assume that the average of the two, or 3510 gallons, would have been adequate to maintain them in a good growing condition. On this basis, during such a summer as 1932 at Wooster, the quantity of water required to maintain 1000 square feet of lawn in a suitable condition would be approximately 8000 gallons. If city water costs 30 cents per thousand gallons, then, with a rainfall-evaporation ratio similar to that of 1932 (0.49 from May–September, inclusive) the expense of water alone in maintaining a lawn in a good growing condition would be $2.40 per 1000 square feet of lawn. Of course, the quantity of water required would vary widely with the season. In some years, the rainfall, evaporation, temperature, and other regulatory conditions might be such that little, or possibly no, watering would be required; whereas in others, similar to 1932, the rainfall-evaporation ratio might be such as to make watering desirable throughout the greater part of the season. The water requirement would vary also with the soil; a sandy soil would require more and a heavy, clayey one less water than a soil of the type of the Wooster silt loam.

Summary

1. After watering artificially at the rates of 1.5, 2.0, and 3.0 times the normal for 5 years, 1927 to 1931, inclusive, the stand of Kentucky blue grass on the artificially watered plots gradually became inferior to that on the plots receiving no water exclusive of rainfall. The grass was progressively more unsatisfactory as the rates of water application were increased. The stand of Kentucky blue grass on the plots not watered artificially remained good.

2. A method of watering employing Livingston's standardized, spherical, black atmometers as the criterion for the time of application and by which it

is aimed to supply enough but not too much water is suggested. The results indicate that on a soil like the Wooster silt loam, grass should be maintained in a good growing condition providing it is watered as soon after a rain as the evaporation from a black atmometer equals 320 cc. of water.

3. On the basis of this method, then in a year like 1932 with a rainfall for the period May to September, inclusive, 66 per cent of the normal, approximately 8000 gallons of water per 1000 square feet would be required to keep grass in a green and satisfactory growing condition. If water is obtainable at the rate of 30 cents per 1000 gallons, then the cost of water required to maintain the proper growth condition would be $2.40 for each 1000 square feet of lawn.

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FLOCK ORGANIZATION OF THE SHELL PARRAKEET *MELOPSITTACUS UNDULATUS* SHAW [1]

R. H. Masure and W. C. Allee

The University of Chicago

Problems centering about the organization of ecological animal communities are deservedly attracting attention. Suggested solutions of such problems in nature depend in the main on inferences drawn from stomach contents, on chance observations of contact reactions, on numbers of animals present, and on natural history lore concerning the habits of the community constituents. It will be long before we can have a fairly exact picture of the organization of a complex animal community under natural conditions.

Among other methods, progress can be made by breaking the problem into simpler elements such that a whole unit can be brought under close observation. Thus the interrelations between members of a flock of birds can be established by observation of appropriately marked individuals. In addition to throwing some light on the problem of ecological community organization in general, such observations also have value in the more restricted field of general animal sociology.

The method first came to prominence from the work of Schjelderup-Ebbe ('22, '23, '31). He found that a flock of domestic hens is organized by what he calls the "peck-order." This means that the rank of individuals within the group is determined by their reaction when another member pecks or threatens to peck them. With hens the organization is definite and the "peck-rights" are not reversed except by combat. We have recently confirmed this work in so far as it deals with the common chicken (Masure and Allee, '34). With the common pigeon we found, however, that while the flock is definitely organized, no one individual has a definite peck-right over another, rather there is a peck-dominance which is shown by one of the contacting birds of a couple pecking more than it is pecked.

The present observations were carried on in conjunction with studies concerning the effect of numbers present on the rate of conditioning in a simple maze. The results of the learning experiments will be reported elsewhere except for pertinent comparisons between speed of conditioning and social rank in the flock. We are concerned here with reporting on the flock organization of the Shell Parrakeet and with comparisons of this organization to that found with the common chicken and pigeon.

In their natural habitat, Australia, Shell Parrakeets assemble in large

[1] This work has been supported in part by a Grant-in-aid from the Division of Biology and Agriculture of the National Research Council.

flocks which may contain as many as a thousand birds. During the breeding season several pairs will be found nesting in one tree and often in the same hollow branch, where the eggs are laid without a nest being built. After breeding these smaller flocks merge to form the large ones already mentioned (Matthews, '16–'17, Vol. 6, p. 477).

In our work, three special lots of birds were observed as well as homo- and hetero-sexual pairs used in learning experiments and a breeding flock in an outdoor aviary. The first two lots consisted of eight birds each, four males and four females; the third was made up of 14 birds, seven of each sex. The two smaller lots were not as instructive as was the largest; data obtained from their study support those from the large flock and, while not given in detail, will be considered when pertinent.

In studying the social organization of birds it is necessary to be able to recognize each individual of the flock under observation. The short legs and quick movements of the Shell Parrakeets made them difficult to distinguish even when tagged with colored leg bands. With practise on the smaller groups, and when the observer was seated near a cage of somewhat limited dimensions, the contact reactions of flocks of seven could be followed with accuracy. Accordingly in the group most studied, we had sex segregated lots of seven birds which were combined to form two different hetero-sexual flocks of six each; one pair was omitted because of the death of one female near the end of the earlier observations. The birds were observed, fed and cared for by Masure alone.

The birds observed were about one year old and were fully mature, since nine months is usually considered to mark the end of immaturity with this species. The special groups under observation were housed in wire cages about four feet long, one foot wide and two feet high; this allowed space for a limited amount of flying. The observations were made in the afternoons when the birds were hungry and while they were feeding from small seed cups placed below the roosting perches. As with chickens and pigeons, the majority of the contacts occurred during the feeding time when the individuals were drawn into close proximity with each other. Actual observations showed sixteen contacts during a half hour's time when the females were not feeding as compared with eighty-three contacts during the succeeding half hour while the birds were feeding. Similar data for the males revealed nineteen contacts before feeding and one hundred fifty-five contacts during feeding. In this report a "contact" is restricted to those times when two birds in close proximity, definitely reacted to each other.

The actual relations between the birds are usually not those of a definite peck-right such as exists with chickens; they resemble, rather, the condition of peck-dominance we have found in pigeons (Masure and Allee, '34). Under these conditions, one cannot predict with certainty the result of any given contact between two birds; after observations for several days, one can, however, predict with much certainty, which of the birds will retreat most often.

The individual that stands his ground most frequently is considered the dominant member of that particular contact pair. The relations differ from those found with the pigeons in that the peck-dominance once established remains fairly steady.

Social Order in Homo-sexual Flocks

There were a few of the contact pairs that showed an absolute peck-right. Among the females after ten days observation, there were ten such pairs in which one had done all the observed retreating; eleven days later, six such pairs remained. With the other four pairs of the original ten, the bird usually subservient had been seen to dominate the contact situation at least once. After these twenty-one days of observation, of twenty-one possible contact pairs, only six showed a definite peck-right. The situation was similar with the males except that only four of the twenty-one possible contact pairs showed no reversals of dominance after twenty-one days of observation.

Four of the six observed absolute peck-rights among the females were exercised over the same individual (Y) which was dominated by all the other members of the group. During the twenty-one days of observation of the sex segregated flock, Y was observed to retreat ninety-nine times and to dominate a contact reaction only three times, once with P and twice with R, both of which ranked high in the social order of the flock. Y only had two "no-decision" contacts, one of which was with P which it once successfully withstood.

The four contact reactions which were not observed to be reversed among the males were exercised by B and by S, ranking members of the male flock over Y, R and Ba. Of these Y was lowest in the social order while Ba and R were clearly dominant over but one bird, G, which also stood low in the social scale. These relationships indicate that only those individuals low in the social organization of the parrakeet flocks, are completely dominated in their reactions with another bird and that even they peck back effectively at times. Not all the low ranking birds are so dominated for among the males, G was subordinate to all other members of the male flock except Y and yet at times G dominated each of its contacting individuals, without counting its thirty-five recorded contacts with Y, G retreated 193 times, dominated forty-six times and engaged in twenty-eight "no decision" contacts.

Due to the fact that the birds were later divided into two hetero-sexual groups, it was possible to re-observe only four of these 10 relationships for which no reversals were seen. Three of the four remained unchanged. The fourth, recorded in the homo-sexual male flock as S:R 4 (chart I) which means that of the four contacts observed, S dominated all, after fourteen days in the hetero-sexual group became 2 S:R 13–5. This means when expanded that S retreated twice from R which it dominated 13 times and there were in addition five "no-decision" meetings. This illustrates a change from what we have called a "peck-right" relationship to one of "peck-dominance."

It is possible that with long continued observation all of the observed cases of peck-right among the parrakeets would have been changed to cases of peck-dominance. It can only be stated that such changes were still being recorded when the observations were discontinued.

CHART I. *Showing the contact reactions of lots of seven females, of seven males and of two heterosexual sets of three pairs each. Each bird is represented by a symbol. G: Y 10–1 means that of 11 observed contacts, G dominated 10 times and there was 1 "no-decision" meeting. 2 R: Y 15 means that of 17 observed contacts, R dominated 15 times and was dominated twice. The number of daily observations is given at the top of each column*

Females	Males	Pairs, Lot A	Pairs, Lot B
21 days	21 days	14 days	14 days
		Hetero-sexual	Hetero-sexual
O:Y 18	B:Y 40–2	O:Y 4–3	3:G 16
B:Y 7	S:Y 24–1	G:Y 10	R:G 15
G:Y 10–1	S:R 4	O:R 12–1	3:O 19
3:Y 13–1	S:Ba 6	P:R 22–1	Y:O 1[1]
P:G 7	1 O:Y 69–6	1 P:Y 27–1	R:O 7–1
B:R 16	7 G:Y 27–1	1 G:R 8–1	1 Y:G 5
2 R:Y 15	3 Ba:Y 4[1]	2 O:S 43 3	4 3:B 45–1
1 P:Y 36–1	21 B:G 55–12	3 P:S 36–1	4 R:B 37–4
2 3:G 9–1	4 R:G 8–2	2 G:S 20–3	8 Y:B 40–3
1 R:G 6	7 Ba:G 19–4	Homo-sexual	Homo-sexual
2 O:G 10 1	7 O:G 63–10	O:G 7 ♀♀	3:Y 39 ♀♀
5 B:G 8[1]	7 S:G 48–5	P:G 18 ♀♀	3 B:G 30–1 ♂♂
7 3:O 22–5	1 Y:R 2[1]–2	P:O 46 ♀♀	1 O:G 5 ♂♂
3 P:O 31–4	3 B:R 21–2	2 S:Y 36–2 ♂♂	1 B:O 8 ♂♂
7 B:O 8[1]	4 Ba:R 5[1]	2 S:R 13 5 ♂♂	3 R:Y 13–1 ♀♀
7 3:B 21–2	5 O:R 7[1]–3	1 R:Y 1[1] ♂♂	3 R:3 7 ♀♀
15 O:R 35–4	3 B:Ba 22–1		
3 B:P 22	5 O:Ba 14–14		
8 R:P 16	11 B:O 64–3		
11 R:3 20–3	8 S:O 26–10		
6 P:3 36–10	2 B:S 8–2		

[1] Peck-dominance apparently undecided.

The flock organization can be visualized more readily if we disregard the exact details just given and summarize rather the relative position which they indicate. Thus for the females we find the situation outlined in chart II. The symbols representing the different birds are arranged vertically at the left with the more dominant individuals at the top and the more subservient ones lower down. The same order is repeated from left to right horizontally. If the symbol is repeated in the body of the checkerboard, it means that the individual at the extreme left had peck-dominance over that bird. The equality sign means that our data do not show which individual was dominant and the minus sign indicates subservience of the bird listed at the extreme left. If the symbol is underlined, no reversals of contact reactions were observed; otherwise reversals were seen and the relationship was one of peck-dominance rather than one of peck-right. In summary it will be seen that among the females, 3, P and R dominated four birds each; B dominated three, including R and P and showed equality with two; O dominated three and showed equality with one; G dominated one and was equal with another while Y dominated

none and in fact, as we have seen before, Y came off victor in three contacts only.

The summary for the lot of sex segregated males is given in chart III. B dominated the others; S dominated all except B and O in turn dominated

CHART II. *Summary of social ranking among a flock of seven female parrakeets*

	Y	G	O	B	R	P	3
3	Y	G	O	B	—	—	
P	Y	G	O	—	—		3
R	Y	G	—	—		P	3
B	Y	=	=		R	P	—
O	Y	G		=	R	—	—
G	Y		—	=	—	—	—
Y		—	—	—	—	—	—

CHART III. *Summary of social ranking among a flock of seven male parrakeets*

	Y	G	R	Ba	O	S	B
B	Y	G	R	Ba	O	S	
S	Y	G	R	Ba	O		—
O	Y	G	=	Ba		—	—
Ba	=	G	=		—	—	—
R	=	G		=	=	—	—
G	Y		—	—	—	—	—
Y		—	=	=	—	—	—

all except B, S and R; it was approximately equal in rank with R. G was dominated by all except Y which was dominated by all except Ba and R, with which it stood on approximately even footing. In the later homo-sexual contacts shown in the hetero-sexual lots, there were no reversals of peck-dominance.

The order of moving down to take food was also recorded. In making these and the other observations, the watcher sat within a foot of the cage in order to distinguish the colored leg bands. Food was placed in the cage in a small container and the birds were left completely undisturbed except for their reactions with each other. The order of arrival of the males is given in chart IV A and of a hetero-sexual group in IV B. Each line represents one day and the first arrival is given at the left. The order of arrival does not necessarily give the order of eating to repletion, a fact which is more easily demonstrated with the sexually mixed flocks.

Comparisons show there is no relation between the pecking order and the order of approach to food. We interpret the order given in chart IV as an

CHART IV. *Order of arrival at food after its daily introduction. A, males; B, hetero-sexual group of which B, G and O are males*

A

G	R	O	B	Ba	Y	
Ba	B	G	O	Y	R	
B	G	R	Y	O	Ba	
B	Y	G	O	Ba	R	
B	G	O	Y	S	R	Ba
Y	B	G	O	S	R	Ba
B	Y	O	S	G	R	Ba
Y	Ba	B	S	O	G	R
Y	B	O	S	G	R	Ba
Y	S	B	O	G	Ba	R
Y	B	S	G	O	R	Ba
Ba	S	O	B	G	Y	R
Y	S	B	O	G	R	Ba
B	S	O	G	R	Y	Ba
Y	S	B	O	R	G	Ba
Y	S	B	G	O	R	Ba
Y	B	O	S	G	R	Ba
Ba	S	B	G	Y	O	R
Ba	B	Y	O	R	G	S
O	B	R	S	Ba	G	Y
B	Y	S	O	R	G	Ba

B

B	O	G	3	R	Y
B	G	Y	R	3	O
G	B	Y	R	3	O
G	B	O	R	Y	3
B	O	G	Y	3	R
B	G	3	Y	R	O
B	G	3	Y	R	O
B	G	3	Y	R	O
O	B	G	3	Y	R
O	B	G	3	Y	R
O	B	R	G	Y	3
O	B	R	G	Y	3
O	B	G	3	Y	R
O	B	G	Y	R	3

expression of the degree of tameness rather than a revelation of intra-group organization; this suggestion will be discussed somewhat in the following section.

SOCIAL ORDER IN HETERO-SEXUAL FLOCKS

After determining the peck-dominance relationships in the sex-aggregated flocks, they were divided into two hetero-sexual lots of three pairs each and observations were continued for fourteen days with results as detailed in chart I and summarized in charts V and VI. The non-breeding females definitely dominated the males of the mixed flocks. This is graphically shown by female Y which was subordinate to all the other females in the homo-sexual flock and in homo-sexual contacts in the mixed flock; yet Y clearly dominated males B and G and won the only observed contact with O. This is the more dramatic in that Y, the lowest ranking member of the female group dominated B, the highest ranking member of the males in forty of the observed fifty-one contacts. If further support is needed, aside from that furnished by the general summaries, it is furnished by the experience of female G which ranked just above female Y yet when placed with males, G outranked all three with which it came in contact, namely, S, R and Y. The subservience of S is most notable for this bird stood next to the top of the peck-dominance order among the males. While dominating these males, female G remained definitely subservient with the other females with which it was associated in the hetero-sexual flock. In all, the females won 367 of the observed hetero-sexual contacts in these non-breeding flocks, lost 27 and engaged in 23 " no-decision " contacts.

The relations about the feeding place give further confirmation. Two of

CHART V. *Summary of social ranking in a mixed flock of three males and three females (Group A)*

	Y	R	S	G	O	P
♀ P	Y	R	S	G	O	
♀ O	Y	R	S	G		—
♀ G	Y	R	S		—	—
♂ S	Y	R		—	—	—
♂ R	=		—	—	—	—
♂ Y		=	—	—	—	—

CHART VI. *Summary of social ranking in a mixed flock of three males and three females (Group B)*

	G	O	B	Y	3	R
♀ R	G	O	B	Y	3	
♀ 3	G	O	B	Y		—
♀ Y	G	=	B		—	—
♂ B	G	O		—	—	—
♂ O	G		—	=	—	—
♂ G		—	—	—	—	—

the three males were always first in coming to the food in these mixed flocks; sometimes all three males came down first. They usually managed to eat a few mouthfuls only before the females drove them away and remained to satisfy their hunger before the males were allowed to return. This behavior is in keeping with the suggestion that the order of approach to food indicates tameness. A cage of females will be much more disturbed by the approach of a man than will a similar cage of males. Also the mature female parrakeet is more noisy and less tractable than is the mature male.

The dominance of the female over the male in a caged pair has been observed for the Red-faced Love Bird, *Agapornis pullaria* (Greene, '92, Vol. I, p. 126), and both Tavistock ('29, p. 182) and Greene ('92, Vol. I, p. 60) record that females of the Blossom-headed Parrakeet, *Psittacula cyanocephala*, dominate their mates outside the breeding season. During the breeding activities, dominance is apparently reversed. Similar reversals have been reported for the Indian Ring-necked Parrakeet, *Psittacula torquata* (Tavistock, '29, p. 170), and for the Rock Peplar Parrakeet, *Polytelis anthopeplus* (Tavistock, '29, p. 257). Schjelderup-Ebbe ('31, p. 96) has observed the same sort of reversals in the half wild *Anas boschas*. Greene ('92, Vol. III, p. 99) records similar reversal of dominance for the Jamaican Amazon (*Amazona collaria*). We have observed this reversal of dominance for a breeding flock of Shell Parrakeets in an outdoor aviary and in a cage in which a pair was rearing young. In both, the males were observed to chase the females back onto the nest without the female showing resistance.

In the Shell Parrakeet, as in most other parrot species, reciprocal feeding by regurgitation, reciprocal billing and preening of feathers, indicate a mated pair of birds. In our observations, any caged pair whether of the same or of different sexes showed such reactions. Actual or attempted copulations were not observed; however, such observations were also lacking for the breeding flock, housed in an aviary, although fertile eggs and young were produced. The homo-sexual groups of four birds showed sexual differences in behavior. Four males caged together reacted as did pairs of males; four females gave practically no such reactions. Hetero-sexual groups of four or six birds in cages 4 x 2x 1 ft. behaved as did groups of four females and showed very few sexual or sex-simulating contacts. Neither of the homo-sexual groups of seven birds showed this type of reciprocal behavior that suggests mating reactions.

The largest group observed, that of ten pairs in the 10 x 6 x 7 ft. outdoor aviary exhibited constant hetero-sexual activity without pseudo-mating, homo-sexual contacts. It appears that increasing the size of the group above two in a limited space tends to lessen the mating-like behavior; greater increase in numbers in a larger space does not have this sex-inhibiting effect. The observed increase in hetero-sexual activity in the outdoor aviary did not result immediately in egg production; the first eggs were laid several months after the birds were introduced into the aviary at a time when, to all appearances, the sexual reactions remained unchanged.

Social Order and Learning Ability

Katz and Toll ('23) found a positive correlation between position in the peck-right and the ability of the common chicken to master a simple problem. We have been studying the effect of numbers present on the ability of our Shell Parrakeets to turn toward the selected color in a simple two-choice problem box. Bailey and Riley ('31) have previously demonstrated that these birds have the ability to learn to respond so to colors. Our experience as regards the possible correlation between social position and learning ability is summarized in table I.

The maze scores shown in table I give the total errors made, the total number of trials and the total time in seconds before the given bird performed in the maze for two successive days without errors. Any movement off the direct route through the proper alley of the simple maze was counted as an error. Females R and Y were inactive in the maze; they remained quiet for successive five minute trials, the maximum time allotted per trial, and their learning ability could not be determined by the methods used. It is evident that with these parrakeets there is no significant correlation between position in the peck-dominance order and ability to learn to run this simple maze.

TABLE I. *Correlation of maze scores with flock position*

Bird	No. dominated	Total errors	Total trials	Total time in seconds
Females				
3	4	191	176	8177
P	4	114	86	1575
R	4		Did not react when in maze	
B	3	106	100	1053
O	3	251	145	1591
G	1	176	70	3201
Y	0		Did not react when in maze	
Males				
B	6	162	109	1858
S	5	228	195	1451
O	3	137	85	994
Ba	1	68	37	1835
R	1	334	176	5603
G	1	70	50	764
Y	0	254	132	5654

Discussion

These observations of the social organization in small laboratory flocks of Shell Parrakeets demonstrate as did our earlier work with pigeons ('34), that Schjelderup-Ebbe's ('31) generalization that despotic relations exist between individuals of flocks of all sorts of birds such that one is always dominant and the other always subservient does not hold (Masure and Allee, '34). With few exceptions, in any given contact pair of parrakeets of the same sex, now one and now the other dominates the chance contacts; in the long run, the same individual usually wins the majority of the combats. This social order, based on so-called peck-dominance, does not differ in many other essentials from that of chickens in which, as a rule, relative social status between two individuals of the same sex, once established remains fixed unless reversed as the result of another crucial combat.

The difference in the social system of pigeons and parrakeets as compared with that of chickens may be due to differences in ability to recognize another individual or to differences in reaction to the individual when recognized. Each of these aspects of behavior can be further analyzed into simpler elements but in the lack of experimental evidence on the point such theoretical analysis of the possibilities is scarcely profitable. The well supported observation that with non-breeding flocks of Shell Parrakeets, the males are much more uniformly subservient to the females than is usual for any member of either sex in relation with flock mates of the same sex, does not help the analysis, since we have no real evidence concerning whether the recognition or the reaction system differs in the two cases. We know that to human observers, it is more easy to distinguish male from female parrakeets than to distinguish between individual males or females. It would be easy to argue from analogy that the same holds true for the birds and therefore the difference in social behavior is due to the greater ease and sureness of

recognition of the other member of the contact pair. Although this is a plausible suggestion, it is not supported by convincing evidence.

With chickens and pigeons, individuals with high rank in the flock order usually had more contacts than did those low in the social scale. The same relation holds with the homo-sexual flocks of parrakeets. The three ranking females had a total of 110 contacts with each other while the three birds at the bottom of the social order had but 38 in the same time and with, presumably, the same opportunities. The three of highest rank had 71 contacts with B, the bird in fourth of the seven positions; the three lowest ranking birds had a total of 35 observed contacts with B although they had the same chance as did the others. With the homo-sexual group of seven males, the three at the top of the social order had 134 contacts between themselves; the three lowest had 54 with each other in the same time. Those highest in rank had 65 contacts with Ba, number four in the male ranking, while the three lowest showed 46 contacts with this individual. These data support our previous conclusion that birds high in the social order meet each other more often than do those at the bottom of the social ranking.

The same tendency is shown for the more dominant females in the reactions listed in chart I for hetero-sexual flocks as compared with the more subservient males. The former had a total of 137 contacts with other females in these mixed flocks while the less dominant males had 101 in the same time. This difference is probably without real significance since in two groups of two pairs each which were also observed, the males met each other 102 times, while the females were meeting 96 times. In the homo-sexual flocks of seven birds each, the males showed 715 contacts and the females in the same time had 478. In this respect the males resembled those of chickens and pigeons which we have observed in that all showed a greater tendency toward more numerous contact reactions with other males in the homo-sexual flock than did the females for their female flock mates.

The general social implications of this work need not be discussed here; they have been adequately treated elsewhere (Allee, '31, '32, '34). With regard to the more general ecological implications, work such as given here indicates that there is probably in nature much more subtle intra-specific organization, particularly in flocking species, than that which is revealed by the well recorded territorial relationships (Allen, '11–'13; Howard, '20). These are related to leadership and subordination, which, while difficult to study in the field, must be considered before we can have a final picture of the organization of an ecological community. As an example of the possible ecological importance of group organization one has only to raise the question as to the survival value of high social position in periods of food shortage or other forms of environmental stress. Observations on kept groups indicates that high ranking birds would be expected to have a better chance of survival. Suggestion of this question at present as applied to natural conditions, only serves to emphasize our ignorance.

Summary

1. Small homo-sexual flocks of Shell Parrakeets show a fairly definite social organization on the basis of peck-dominance.

2. In non-breeding hetero-sexual flocks, the females are dominant over the males. In breeding and nesting birds, the males are dominant.

3. The order of approaching food in the presence of an observer appears to be related to the degree of tameness rather than to the peck-dominance order.

4. There is no significant correlation between the peck-dominance order and scores made in learning to run a simple maze.

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CONCERNING A GEOLOGICAL EXPLANATION OF THE ORIGIN AND PRESENT DISTRIBUTION OF THE NEW JERSEY PINE BARREN VEGETATION

H. J. Lutz

School of Forestry, Yale University

The Pine Barrens of southern New Jersey have long been regarded by botanists as of high scientific interest; indeed, few other areas in North America have attracted such long-continued and widespread attention. In an attempt to account for the origin and present distribution of the pine barren vegetation Harshberger ('11, '16) and Taylor ('12, '15) developed a geological theory which seems to have been widely accepted. During the course of ecological work within the so-called "Plains," which are included in the Pine Barrens, the writer had occasion to inquire into the geological history of the region. It was surprising to find that the geological facts as now understood are quite different from the ideas which formed the foundation of the geological explanation of the origin and occurrence of the Pine Barrens as developed by Harshberger and Taylor. The purpose of this paper primarily is to show that the Harshberger-Taylor theory was based upon geological hypotheses which are no longer tenable. First, however, it seems desirable to trace the development of the theory from its beginning.

Hollick (1899, 1900) evidently was the first writer who attempted to correlate the occurrence of the New Jersey Pine Barrens with underlying geological formations. He was of the opinion that the Pine Barrens were coextensive with the area of Tertiary sands and gravels. However, the first accurate map of the Pine Barrens, drawn by Stone in 1911, clearly shows that the area of the barrens is not coextensive with the area of Tertiary sands and gravels as Hollick suggested. Indeed, Stone ('11) may have had Hollick's work in mind when he wrote, "Some attempt has been made to correlate these areas or parts of them with underlying geological formations, but a more accurate knowledge of the distribution of their plants shows that such correlation is not possible. The surface soil has far more to do with the matter than the underlying geological formation. The western boundary of the Pine Barrens is often the eastern edge of the cretaceous formation, but in the southern part of the state it is not so, the cretaceous lying in some places fifteen or twenty miles west of the Pines. In the same way the very distinct coast strip with its West Jersey flora is geologically the same formation as the Pine Barrens."

Harshberger ('11) expressed views similar to those of Hollick and stated that, "The geologic formations to the south and southeast of a line drawn

from a point below Long Branch [New Jersey] to another near the head of Delaware Bay are Tertiary, while those to the north of it are Cretaceous. The Tertiary soils extend southward along the Atlantic Ocean to Florida and are occupied by a pine barren flora." As already pointed out the area of Tertiary sands and gravels in New Jersey definitely is not coextensive with the area of Pine Barrens. Going even further, Harshberger ('11) presented the following notion: "During the Pensauken submergence of the New Jersey geologists which occurred prior to the glaciation of the northern hemisphere, New Jersey was depressed to such an extent as to drown the Delaware River at its lower end, allowing the sea to pass up its valley and over the peneplain which had been developed during the previous cycle of erosion, so that a broad sound was formed which connected Raritan Bay with Delaware Bay, forming an island covered perhaps with pine barren vegetation. The mouth of the Delaware River during the post-Pensauken uplift was transferred to Delaware Bay followed by a cycle of erosion which lasted until the ice of the last glacial epoch invaded the northern portion of the state. It was during the post-Pensauken uplift that the flora of the lower Delaware Valley and the coastal strip was probably developed, so that the New Jersey pine barrens became surrounded by a fringe of vegetation developed along similar lines in the coastal strip and along the east and west banks of the Delaware River. . . . During the Pensauken submergence, southern central New Jersey was a sea island separated from northern New Jersey by Pensauken Sound."

Taylor ('12, '15), evidently under the stimulus of the work of Hollick and Harshberger, elaborated the theory of a geological explanation of the origin and present distribution of the Pine Barrens. The general ideas involved may be summed up in Taylor's own words as follows: "For the phytogeographer the salient features of these changes are that the Beacon Hill [formation] has been uninterruptedly out of the water since upper Miocene times, and that it has several times been partly, and often entirely surrounded by water. These facts, together with the encroachment of the glacier, and its recession, with the probable deposition of a great deal of morainic material around Beacon Hill, makes this formation the oldest in New Jersey, either on the coastal plain or in the glaciated regions northward, that could have been continuously covered with vegetation. This, it seems to me, is why the Beacon Hill formation is the controlling factor in the origin and present distribution of the pine-barrens. The area of the pine-barrens (see fig. 1) is not exactly coextensive with Beacon Hill (see fig. 2) but the differences are so slight that recent and local erosion of the formation would account for the failure of the two regions to superimpose, as it were.[1] In other words the New Jersey pine-barrens exist exclusively on this Beacon Hill formation, an area isolated by geological processes, and maintaining a relict, or climax flora, the antiquity of which greatly antedates any of the rest of our vegetation

[1] Figures 1 and 2 in this paper are essentially the same as figures 1 and 2 of Taylor ('12).

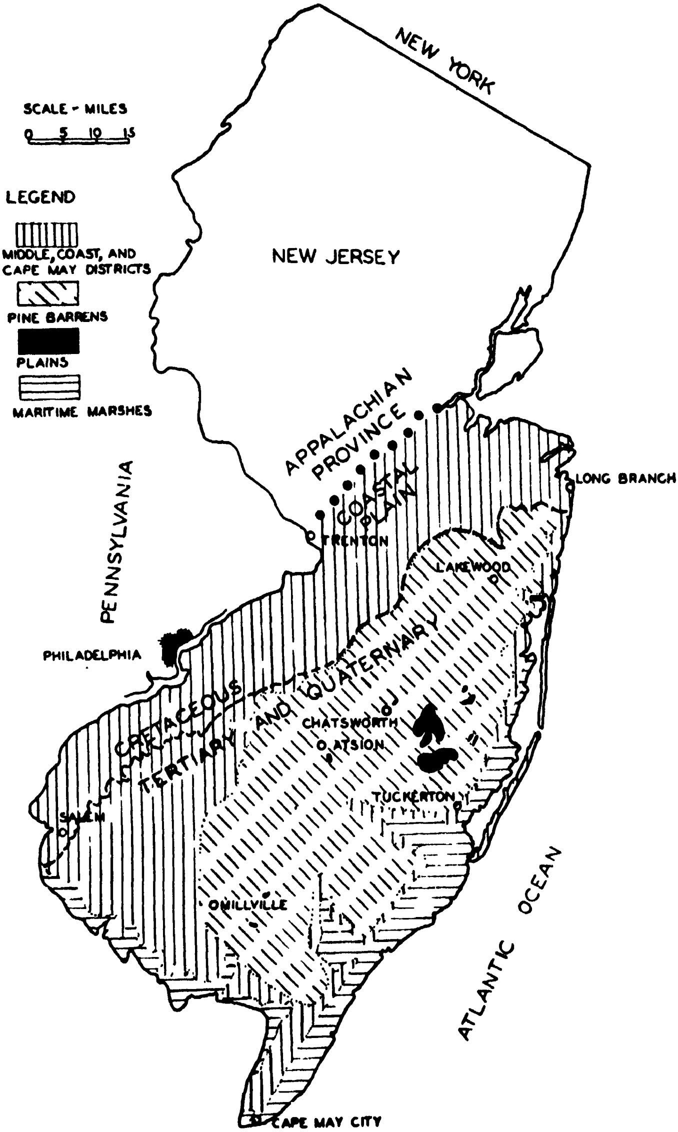

FIG. 1. Map showing the location of the Pine Barrens in relation to other plant communities. The boundary between the Cretaceous formations and the Tertiary-Quaternary formations is indicated. Adapted from Stone, 1911.

hereabouts, so far as permanency of position and phytogeographical isolation are concerned. This undoubtedly accounts for the composition of the flora, . . . All of these evidences,—the geological history of the country, the isolation of Beacon Hill and the consequent isolation of the ancient pine-barren flora upon it, the post-glacial migration of some of the pine-barren species,

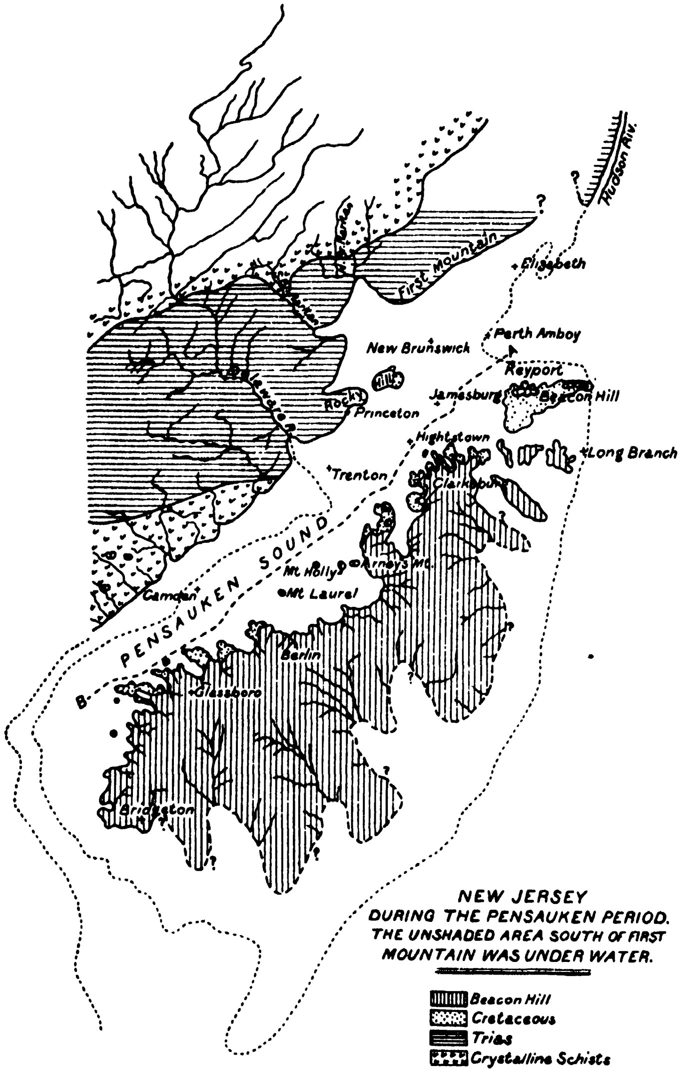

FIG. 2. Map of the Beacon Hill area as outlined by Salisbury. Copied from plate 12 of Salisbury's report, 1898.

and finally the present distribution of the pine-barrens, coinciding as it does so closely with the Beacon Hill formation, seem incontestably to point to a geological explanation of the origin and present distribution of the pine-barrens."

This elaborated theory was subsequently discussed by Harshberger ('16) who was in full agreement with it. He combined figures 1 and 2 (referred to by Taylor, '12) and was impressed by the "unusual coincidence." To quote: "Thus, if we contrast the area occupied by the Beacon Hill formation

and the area in central New Jersey covered by the pine-barrens, we find an unusual coincidence. . . . This coincidence of the two areas is made clear when we remember that the Beacon Hill formation was an island during the Pensauken submergence and that it was covered with vegetation of the pine-barren type. The location of the present pine-barren area is due to this fact, to the present soil conditions, and to the fact that when the land surface was again elevated after the Pensauken submergence the deciduous types of vegetation invaded the recently elevated land in the coastal plains of Delaware, Maryland, and New Jersey, so that the pine-barren vegetation was surrounded on all sides by deciduous forests. The deciduous forests, on the other hand, were unable to supplant the pine-barren vegetation, because the latter had reached a climax condition. Both types of vegetation in the New Jersey coastal plain were mutually exclusive."

Both Harshberger and Taylor obtained their geological data from Salisbury (1898) and in this they should not be criticized. Salisbury's report was then regarded as the best information available. However, it is a fact, as will be shown presently, that subsequent field work (completed in 1903) convinced Professor Salisbury himself that the views expressed in his 1898 report were not tenable.

There is some confusion in the matter of terminology since the earlier reports of the New Jersey Geological Survey (1892–1900) included the Cohansey sand in the Beacon Hill formation and referred the combination to the Miocene period. The present view may be set forth by Salisbury and Knapp ('17) as follows: "Above the beds definitely correlated with the Miocene, there is another pre-Quaternary formation, or perhaps two formations. . . . This formation (or the older of the two if there be two) is the *Cohansey sand,* the age of which has not been definitely determined; but it is probably late Miocene or Pliocene. In some places, the Cohansey sand is overlain by gravel, which has been called, in various annual Reports of the Survey, the *Beacon Hill gravel.* Whether it is to be regarded as the upper part of the Cohansey formation, or as a separate formation, is an open question." Lewis and Kümmel ('15) were inclined to regard both the Cohansey and Beacon Hill formations as of Pliocene age.

In 1898 Professor Salisbury held to the marine or estuarine origin of the Pensauken formation and consequently it was necessary for him to postulate a rise of the sea level at least as great as the elevation of the present surface of the Pensauken formation between Trenton and Raritan Bay. His later work raised serious doubts as to the marine or estuarine origin of the Pensauken and caused him to change his earlier view. In 1917 Salisbury (with Knapp) stated his final position as follows: "On the whole, the belief is entertained tentatively, that rivers were the agents chiefly concerned in the depositions of the formations [Pensauken], and that such part (if any) of it as is marine is very subordinate. . . . It is not known how high the land stood

relative to sea level in either epoch [Bridgeton and Pensauken]. *No shore lines are to be found, and no fossils are available.*" [2] Recent studies by Campbell and Bascom ('33) have led definitely to the conclusion that the Pensauken gravel was deposited on the land; they maintain that these gravels were deposited as a thin sheet in a broad river valley.

Returning now to the Harshberger-Taylor theory, it will be shown that it was based upon certain fallacies, among which the following may be mentioned:

1. That the Pine Barren area is practically coextensive with the Cohansey-Beacon Hill formation (the Beacon Hill of earlier writers).
2. That plate 10 (facing p. 102) and plate 12 (facing p. 130) of Salisbury's 1898 report represent the facts. (Salisbury's plate 12 is here reproduced as figure 2.)
3. That the alleged water barrier to the west and north resulted in isolation of the vegetation on "Pensauken Island."

That the Pine Barrens are not even approximately coextensive with the Cohansey-Beacon Hill formations is readily apparent upon comparison of Stone's map (fig. 1) with a good geologic map such as that accompanying Lewis and Kümmel's 1915 report. Within the pine barren region one may note the occurrence of Kirkwood beds, *e.g.*, west of Asbury Park and east of Pemberton. The Bridgeton formation outcrops in the barrens northeast of Batsto and is very common in the southern part of the region; Pensauken beds support pine barren growth over a considerable area northwest of Toms River. The Cape May formation outcrops in the barrens south and west of Tuckahoe and at various places along the coastal strip. Most significant of all, however, is the fact that in the southwestern part of the State the West Jersey forest flora (deciduous hardwoods for the most part) greatly encroaches upon the Cohansey and Bridgeton formations. The statement of both Harshberger and Taylor to the effect that the pine barren area is practically coextensive with the Beacon Hill formation (now recognized as Cohansey and Beacon Hill) is incorrect. Their view in this respect is just as erroneous as was the suggestion of Hollick that the Pine Barrens were coextensive with the Tertiary sands and gravels. The fact seems to be that the Pine Barrens are not coextensive with any particular geological formation. Stone ('11) correctly observed, "In West Jersey, moreover, we find considerable differences in the flora of different parts of the same formation. In the cretaceous, for instance, we have in the rich marl beds one style of vegetation, while on sand deposits of the same age are plants of quite a different sort." Again, in speaking of the outlying "islands" of pine barren vegetation in the Middle or West Jersey district it appeared to Stone that, "There seems to be no peculiar geological formation correlated with these outlying colonies except that dry ground species are found where deposits of

[2] The italics are the present writer's.

pure white sand or gravel occur, but which are not necessarily of the same age as similar deposits in the Pine Barren area proper."

Passing now to the hypothetical " Pensauken island " of Salisbury (1898) and figured in his plates 10 and 12 (see fig. 2 of the present paper), it need only be said that it had no basis in fact. As indicated earlier, Salisbury and Knapp ('17) in referring to the Pensauken period make the unqualified statement that, " It is not known how high the land stood relative to sea level in [the Pensauken] . . . epoch. No shore lines are to be found, and no fossils are available." Yet the " Pensauken island " occupies an important place in the Harshberger-Taylor theory. Both writers figured the " island " in their papers and both stressed the fact that its area was nearly coextensive with the area of the Pine Barrens. The approximate coincidence noted was entirely accidental and consequently without significance.

Both Harshberger and Taylor held to the view that the vegetation on " Pensauken Island " was isolated by the alleged water barrier to the west and north. For the sake of argument, let us for the moment ignore the fact that in 1917 Salisbury discredited the existence of this island which he " created " in 1898 and assume that such an island did exist just as indicated in figure 2. At several points along the west side the indicated water barrier would be only ten to fifteen miles wide. Surely this could not constitute much of a barrier to plant migration over an extended period of geological time. Ostenfeld ('29) in discussing the origin of the flora of Greenland stated, ". . . even in more southerly localities West Greenland has received a fair contingent of American species, especially the sub-arctic and boreal types, which must have come across Davis Strait [roughly 175 miles], probably chiefly from Baffin Land and Labrador. . . . A distance like the one across Smith Sound [roughly 25 miles] is nothing when there is a cover of ice." It is of further interest, again following Salisbury's 1898 report, to read that, " Northwest of the main island, Arney's Mount, Mount Holly, Mount Laurel, Big Mannington Hill and a few isolated points, which had remained as monadnocks on the pre-Pensauken peneplain, were not submerged, but they constituted small, low islands. In Monmouth county there were likewise several islands northwest of the large one." The Harshberger-Taylor theory of isolation fails completely to explain why these scattered points—allegedly islands during Pensauken time—should at present be occupied by deciduous forest vegetation instead of pine barren vegetation. According to Salisbury's 1898 report these islands had the same geological history as his large " Pensauken island."

In summation it may be stated that the Harshberger-Taylor geologic explanation of the origin and present distribution of the New Jersey Pine Barrens lacks one fundamental and essential requirement—namely, a sound geological basis. It is the writer's conviction that the theory cannot stand in the light of present-day geological information.

As a matter of fact an elaborate theory is not required to explain conditions within the Pine Barrens. Both origin and present distribution of the pine barren vegetation may be accounted for rather simply. Its origin may be reasonably explained by the views of Kearney (1897), Small ('24), Fernald ('31), and others. Fernald ('31) expressed the idea concisely in the following words, " Then, with the Tertiary uplift of the Appalachian region and its final conversion into a vast well-drained mesophytic area available to the groups which now constitute the climax forests of the Appalachian Upland, the Cretaceous xerophytes and hydrophytes which had previously occupied the ground gradually moved out to the newly available and for them more congenial coastal plain and similar habitats to the west and northwest." The present distribution of the Pine Barrens in New Jersey is best explained on the basis of contemporaneous edaphic, climatic and biotic conditions, to which may be added pyric and anthropeic influences which have been important during the recent past.

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THE SPACE FACTOR IN THE GROWTH RATE OF TADPOLES

Roberts Rugh

Columbia University Zoology Laboratory

There are numerous environmental variables which directly and independently effect the growth rate of tadpoles. The principal factors are, (1) temperature of the medium, (2) amount of available food, (3) amount of radiant energy through light, (4) amount of surface and available oxygen, (5) amount of accumulated excretory wastes, (6) amount of bacterial growth, (7) amount of available volume per individual, (8) amount of available space per individual, (9) amount of forced or stimulated exercise, (10) presence of growth inhibiting substances, X-substances, or autotoxins.

In any experimental work involving tadpole growth rate, all of these variables must either be eliminated or controlled. Of all of the variables listed above, the space factor has not been adequately recognized or evaluated in respect to aquatic forms. According to Allee ('31), Hogg ('54) was the first to note the limiting effect of volume on the growth rate of aquatic forms; Semper ('74, '81) suggested that this retardation of animal growth might be due in part to the mechanical disturbances conditioned by crowding; De-Varigny ('94) suspended glass tubes measuring 2 to 3 cm. in containers of various sizes, the tubes being closed over the bottom with muslin. In each tube he placed a single specimen of *Lymnaea stagnalis* and concluded from results that the growth variations depend on total volume, surface area, and the accumulation of faeces, rather than space. Crabb ('29) stated that food, foul media, and crowding all effected the growth rate of these pond snails.

In respect to the tadpole, with which this paper is concerned, Yung ('85) stated that the dwarfing of tadpoles in crowded conditions was due to insufficient aeration; Bilski ('21) found that frequent changes of water or crowding would retard the growth rate of tadpoles of *Bufo* and *Rana esculenta*. A corollary to crowding is an increase in the number of frequency of contacts, and it was to this stimulated exercise that Bilski attributed retardation in growth rate. On the basis of these observations, and those of Semper on snails, Bilski devised the following formula to express growth as inversely proportional to group stimulation (see Allee, '31, p. 115, for derivation):

$$y = K\left(\frac{\sqrt{x}}{x-1}\right),$$

where y = size, x = number of animals in a given space, and K is a constant. Goetsch ('24) found that when the food variable was controlled, the accumu-

lation of excretory wastes played only a secondary rôle to the major variable of more frequent collisions in a denser population of tadpoles. Adolph ('31) failed in the attempt to apply Bilski's formula (above) to all stages of tadpole growth and accounted for this by suggesting that crowding and agitation discourage the assimilation of food. He further pointed out that the body weight is denied the tadpoles in proportion to the square root of the density ($\sqrt{n}$) because the number of random collisions within a unit of time would be proportional to ($\sqrt{n}$).

When there are such differences of opinion in respect to the effect of the variables; space, volume, and excretory wastes, it is no wonder that Allee ('31) writes: "When one attempts to summarize the evidence concerning the factors causing the retarded growth in crowded conditions, he finds a decided lack of unanimity among the different investigators, indicating that in all probability there are many factors which may produce the same results" (p. 118).

Apparatus and Experiments

A simple apparatus was devised to eliminate all of the experimental variables listed above except the *space factor.* The apparatus consisted of ten-inch finger bowls, each divided into equal compartments by fine-meshed galvanized wire screens. The bottom of each dish and the cut lower edges of the screen were covered with pure paraffin. Frog eggs (*Rana pipiens*) were secured in the laboratory in the manner recently described (Rugh, '34) and were selected at the four-cell stage. The eggs were separated from each other and were placed in the various compartments, the number of eggs varying in order as follows: 3–10–3–25–3–10–3–25. On every fourth day the water was changed until after the twelfth day when food was first added. Water was changed daily from the twelfth until the thirtieth day, the last day of the experiments. The food consisted of a pipetteful of a concentrated suspension of liverwurst added daily to each compartment, after which the entire dish was agitated for a short time. The quantity of food added was more than adequate for all of the tadpoles, and since a complete change was made daily, it is assumed that optimum food conditions were available for all tadpoles. Liverwurst was used because it was necessary to avoid the variables accompanying the use of plant food.

This simple apparatus is so devised that all of the above mentioned variables except the space factor are either eliminated or equalized. Diffusion continuity equalized the normal variables of food, temperature, concentration of metabolic wastes , X-substances or autotoxins, bacterial growth, and total volume. Radiant energy through light was equal for all tadpoles and control experiments in total darkness showed that any slight imperceptible variations were negligible, for the same proportional results were secured in total darkness. The amount of space per individual and, collateral with this, the

amount of stimulated exercise through crowding, were the controlled variables with which these observations were concerned.

A total of eight complete sets of readings were made, after thirty days of growth. The average of the readings, representing 646 tadpoles in all, is given in tabular form below:

	Number of Tadpoles Per Unit of Space		
	3	10	25
Length (total) in mm.	25.23	20.90	17.24
Breadth (body) in mm.	6.55	5.78	4.30
Length (body) in mm.	9.46	7.93	6.09

The accompanying graph (fig. 1) represents a rapid decline in the growth rate between the numbers 3 and 10 per unit of space, with a less rapid decline

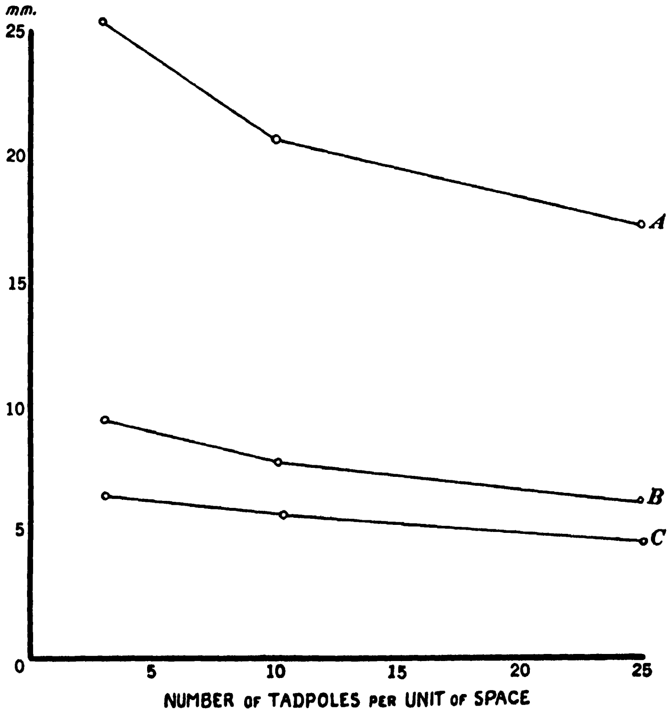

Fig. 1. Growth rates of tadpoles with different numbers per unit of space. *A*—total length (body and tail); *B*—body length; *C*—body breadth.

between 10 and 25 per unit of space. The accompanying photograph (fig. 2) represents actual experimental tadpoles taken at random from respective compartments, and they indicate very clearly differential growth effected by available space.

Fig. 2. Pairs of experimental tadpoles taken at random from compartments containing 3, 10 and 25 tadpoles each.

Discussion and Conclusions

In any experiment of this nature it is not a simple matter to isolate the space factor, eliminating the stimulating factor of more frequent collisions in the more crowded populations. The presence of other individuals is, of course, a corollary to variations in available space. It has been impossible to fit the above data to Bilski's formula. The data in this paper tends more to support the contention of Adolph ('31) that size variations, with the space factor alone considered, can be most accurately calculated on the basis of $\sqrt{n}$ since this expresses the probable frequency of collisions. There is no doubt that collisions provide the most frequent and effective stimulus to activity and that the sudden, rapid movement of the tadpole must of necessity involve the expenditure of energy which otherwise might be expressed in terms of increased size.

Numerous attempts have been made to draw an analogy from land mammals and even from human society, with the suggestion that racial or national differences in stature may be an expression of variations in available space. However, the factors in the environment of a mammal are, no doubt, so much more numerous, variable, and complex, than in the environment of the tadpole, that such analogies can have no biological import.

The tadpole is sensitive to many variations in its particular environment and may express this sensitivity by a differential rate of growth. In this paper there has been presented experimental evidence that the *space factor,* with its corollary, the increased opportunity for collisions with reduction in space per individual, is of considerable importance in any experiments where the growth rate of tadpoles is considered.

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THE PENETRATION OF RAINFALL THROUGH HARDWOOD AND SOFTWOOD FOREST CANOPY

H. W. Beall

Forest Service, Ottawa, Canada

In connection with a study of forest-fire hazard being conducted at the Petawawa Forest Experiment Station of the Dominion Forest Service, Department of the Interior, Canada, at Chalk River, Ontario, an investigation was made, during the 1933 fire season, of the proportion of the rainfall recorded in the open which reaches the forest floor under stands with nearly full canopy.

Measurements of rainfall in the open were made at the meteorological observation station operated at the Petawawa Forest Experiment Station. A non-recording gauge of conventional pattern was used for comparison with similar gauges in the forest. The rims of all gauges were about six inches above the ground. Readings were made twice daily in the open, and once a day in the forest.

A softwood stand typical of the region was selected about one mile east of the point where the meteorological equipment was located. This was of mixed white and red pine (*P. strobus, P. resinosa*), 40 years old, with a crown density of 96 per cent as determined by the Clement's photometer. Within an area of 100 square yards in this forest, five rain gauges were disposed as follows:

One gauge directly beneath a small, natural opening in the canopy.

Two gauges under points in the canopy representing as nearly average conditions as possible.

Two gauges each about one foot away from the trunks of average trees, one on the north side of a tree and one on the south.

In was considered that the average of these five gauges would give a fair representation of the amount of rain penetrating the canopy generally.

Five gauges were similarly placed in an uneven-aged forest of mixed tolerant hardwoods, consisting mainly of beech (*Fagus grandifolia*), maple (*Acer saccharum*), and yellow birch (*Betula lutea*), with 97 per cent canopy, about 500 yards south of the meteorological equipment.

Readings were taken from May 3 to October 23, inclusive, and an unusually wide range of rainfall conditions was covered. The table shows, by monthly as well as seasonal averages, the amount of rain falling in each gauge in the forest, expressed as a percentage of the corresponding rainfall in the

open. Individual rains were not compared, owing to the considerable distances separating the field stations from the control gauge. Humphrey ('33) has shown that individual rains may vary considerably over relatively small areas, consequently the month was taken as the shortest period for satisfactory comparison.

TABLE I. *Relation between rainfall under canopy and in open*

Period	Rainfall in open (inches)	Rainfall under canopy (per cent of rainfall in open)											
		Softwood forest						Hardwood forest					
		Gauge under opening	Gauge under avg. cover (1)	Gauge under avg. cover (2)	Gauge at N. side of tree	Gauge at S. side of tree	Average all gauges	Gauge under opening	Gauge under avg. cover (1)	Gauge under avg. cover (2)	Gauge at N. side of tree	Gauge at S. side of tree	Average all gauges
May (3d to 31st)	2.48	105[1]	77	92	33	33	68	89	100[1]	98	67	73	85
June	1.27	80	60	65	40	31	55	75	94	79	72	61	76
July	6.85	68	68	82	58	52	66	82	86	88	74	73	81
August	1.77	104[1]	67	80	35	40	65	80	91	95	69	68	81
September	2.00	93	58	75	32	33	58	76	84	71	67	51	70
October (1st to 23d)	1.26	87	56	69	25	36	55	79	78	83	64	67	74
Season	15.63	84	66	80	44	42	63	81	88	87	71	68	79

[1] Percentages of 100 or more are probably due to the location of "drip points" adjacent to the gauges. That they are not due to unequal rainfall distribution over the stands is indicated by the figures for the other gauges in the same months.

While these figures are based on only one season's data, and must, therefore, be accepted with some reserve, several inferences worthy of note may be drawn from them.

In the white and red pine forest, roughly 60 per cent of the season's rain reaches the forest floor, as compared with about 80 per cent in the hardwood stand—this in spite of the fact that the density of canopy is practically identical in the two sites, as measured by the photometer. Several reasons may be advanced for this discrepancy. It is suggested, among others, that the softwood species generally afford a much greater number of sharp angles and small rounded surfaces in both foliage and twigs than do the hardwoods. Water droplets having small radii of curvature and therefore capable of accumulating to a considerable mass may be held at these points, whereas the flat, smooth surfaces of hardwood leaves and twigs shed the droplets readily.

In a pure white pine forest with 96 per cent canopy, one mile south of the hardwood stand, a single gauge placed under average canopy conditions caught, from June 1 to October 23, 57 per cent of the rainfall in the open. This agrees reasonably closely with the results in the mixed pine stand, par-

ticularly in view of the fact that the white pine crowns are slightly deeper than the red.

The Lakes States Forest Experiment Station ('29) found that 80 per cent of the total rainfall reached the ground in both a hardwood-hemlock forest and a jack pine forest. While the density of canopy is not stated, it is reasonable to suppose that the jack pine stand was considerably more open than the more tolerant mixture of red and white pine.

No pronounced difference is indicated between the rainfall in the small gaps in the crown cover, and that under average canopy conditions. Such differences as occur seem to be largely related to other factors, such as the location of " drip points " overhead.

The rainfall close to the trunks of trees is in every case, however, markedly lower than elsewhere. This is particularly true in the softwood forest, where the average is 34 per cent lower than that of the other three gauges. The trickle of rain down the trunks themselves was, of course, not included in these measurements, and from the standpoint of the moisture content of forest-fire fuels it is not of great consequence. The amount of precipitation which reaches the ground along branches and trunks has been set at about 2 per cent for softwoods and 15 per cent for hardwoods (Zon, '27).

There is little evidence to show that on months with the highest total rainfall the greatest percentage penetrates the forest canopy. This factor seems to be more closely related to individual rains.

Contrary to the findings of the Lake States Forest Experiment Station ('29), the data do not show any marked influence of the presence or absence of hardwood foliage on the percentage of rainfall reaching the forest floor. During the greater part of May and the latter part of the period covered in October, there were practically no leaves on the hardwood trees. Yet the average penetration for these months is 79 per cent as compared with 77 per cent for the four intermediate months. In figure 1,

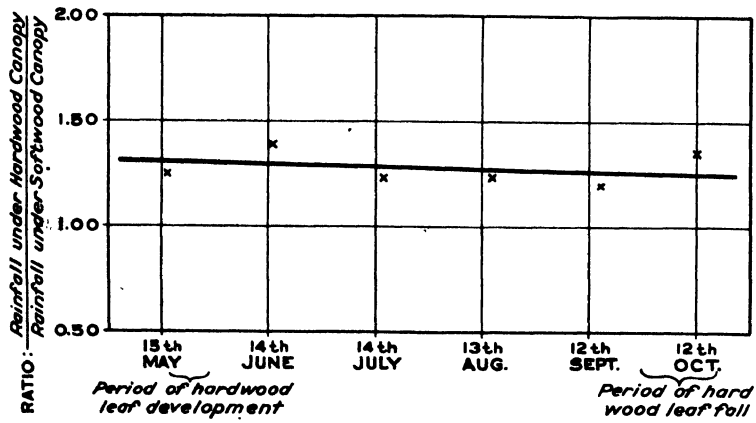

FIG. 1. Ratio of rainfall in hardwood forest to rainfall in softwood forest, in monthly totals. May 3 to October 23, 1933.

$$\text{the ratio } \frac{\text{rainfall in hardwood forest}}{\text{rainfall in softwood forest}}$$

is plotted for each month. If we assume that the canopy in the softwood stand remains unchanged, which for practical purposes is sufficiently correct, the change in hardwood canopy will be seen to have a negligible effect, since the change in ratio shows practically no seasonal trend and is, in fact, quite small throughout the season.

The inference is that a relatively light rain is sufficient to moisten the surface of the leaves, after which the drip from them takes place about as fast as the rain falls.

Summary

In the pine forest about 60 per cent and in the hardwood forest about 80 per cent of the total rainfall reaches the forest floor, exclusive of the water which runs directly down the trunks.

Rainfall close to the trunks of trees is considerably lighter than in other parts of the forest.

The presence or absence of foliage on hardwood trees does not, with the probable exception of very light rains, materially affect the percentage of rainfall penetrating the canopy.

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DISTRIBUTION OF ANT SPECIES IN THE CHICAGO REGION WITH REFERENCE TO ECOLOGICAL FACTORS AND PHYSIOLOGICAL TOLERATION

MARY TALBOT

Whitman Laboratory, University of Chicago

ECOLOGICAL SURVEY

Introduction [1]

This study of the distribution of ants was made within a radius of ninety miles of Chicago in a number of available communities. The oak-hickory and beech-maple woods contain an essentially northeastern fauna while the prairies bring in western forms and the dunes contribute a few distinctly southern species.

The purpose of the work was two fold: (1) to make a survey of the ant distribution of the area, correlating this distribution with the recognized plant communities and (2) to make certain experimental studies with reference to the toleration of ants to extremes of heat and dryness in order to ascertain whether these could be shown to be limiting factors in distribution. In most of the work ants of one genus were used in order to determine whether adaptive differences could be demonstrated between species.

Ants were studied in the various recognized stages of plant associes to ascertain, not only the distribution of various species, but to determine whether this distribution fits that of the plant communities. It is believed that if sufficient groups of animals: ants, spiders, snails, mammals, etc., are studied through the steps of ecological succession, and if these studies are later gathered together, as complete a picture of animal succession may be shown for the region as has already been described for the plants. Ants are especially favorable animals for this study because they are abundant in numbers (but do not have so many species as to complicate the work too much), their nests are permanent over a number of years and are found in fairly definite habitats, and ants of one species or another occupy almost every niche. In addition, W. M. Wheeler ('32) states that, "Ants are so extremely sensitive to the degrees of temperature and humidity of their environment and to the character of its vegetation that many species or subspecies are confined to very narrow ecological habitats."

[1] Identifications of most of the ants were kindly checked by Dr. M. R. Smith; *Myrmica* by Dr. Neal Weber. I wish also to express my appreciation for help from Dr. A. E. Emerson, Dr. C. H. Kennedy and Dr. W. C. Allee.

Ants were collected (table I) over a period of three years from the following locations:

(1) The dunes of the south and southeast shores of Lake Michigan at such places as Miller, Ogden, Tremont and Furnaceville, Indiana; and Lakeside, Michigan; (2) Oak woods on moranic clay at Palos Park and New Lennox, Illinois; and Valparaiso, Indiana; (3) Beech-maple climax woods at Joliet, Illinois; Smith and Turkey Run, Indiana; and Warrens Woods and Lakeside, Michigan; (4) Prairie southwest of Chicago; (5) Roadsides and pastures at various places. Turkey Run, in central Indiana, is south of this general range but no species are included from there which are not also found in one of the more northern locations.

General Description of the Region

The area can be divided roughly into three main successions according to the nature of the substratum: sandy deposits along southern Lake Michigan; upland moranic clay laid down by glaciers; and the prairie soil to the southwest. The dunes show a clear-cut succession from the early pioneer stages of fore-dunes, poplar dunes, and pines, through the black oak and red-white oak associes, to the beech-maple climax. On clay the majority of the woods are in some stage of oak succession. This is typically a red-white oak associes merging into oak-hickory in some places. This succession also leads to a beech-maple climax. Prairie reaches almost its eastern limit here and is not extensive. It is the climax condition, passing through stages of bog and low prairie.

Plant successions for the region have been unusually well worked out (Cowles, '01, and Fuller, '25); animal communities have been studied to a less extent (Shelford, '13, Holmquist, '26, Park, '30, and Pearson, '33); and some valuable environmental data have been recorded (Fuller, '14, and Park, '31).

Distribution

Extensive sand dunes have been formed along the southern shores of Lake Michigan. Near the lake the sand ridges are still in a very unstable condition. Moving dunes and blowouts are common but in most places the dunes are caught and held by sand-binding grasses, shrubs, and poplar trees. Further back the dunes become stable and thoroughly wooded, first with pines, then with oaks. This makes an unusually clear-cut succession of ecological habitats and gives an exceptional opportunity for correlating distribution with environmental differences (fig. 1).

Beach.—The flat beach consists of almost bare sand with a few pioneer herbaceous plants forming a sparse vegetation. Ants cannot become established here.

Fore dunes.—Behind the beach the fore dunes rise fifteen or twenty feet. They are out of reach of even winter storm waves and so can begin to acquire

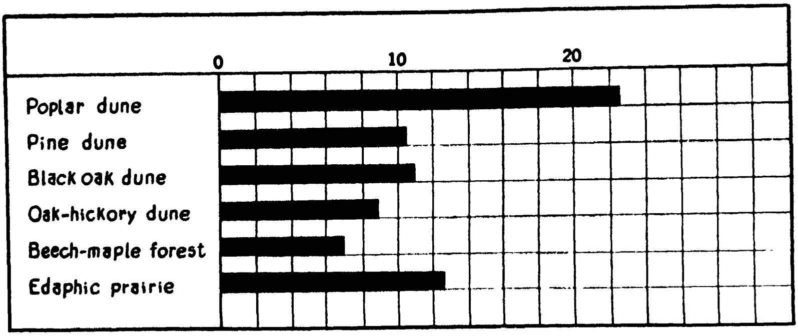

FIG. 1. Comparative mean average daily evaporation in plant communities of Chicago area (modified from Fuller, '14).

a permanent vegetation. Such xeric plants as the sand grasses (*Calamovilfa longifolia* Hack and *Ammophila arenaria* Link), bushy willows (*Salix* sp.) and the sand cherry (*Prunus pumila* L.) tend to hold the sand in some places. But even in patches of sand cherry and willow the sand is blown about to considerable extent. In bare areas it is being almost constantly shifted.

The fore dunes are not a very suitable place for ants, partly because of this instability. Ant nests are maintained for a number of years and usually depend upon a stable substratum. Great extremes of temperature and moisture and lack of diversity of food and habitat are also limiting factors in the fore dunes. Sand is the only habitat which may be relied upon to be present and so the characteristic ants of the fore dunes are the crater-forming *Lasius niger neoniger* and *Pheidole bicarinata*. Colonies are not common and exist only near the roots of grasses or sand cherry and are usually found on slopes away from the lake, which is on the windward side. In addition to these species, an occasional pioneer colony of log dwelling ants can be found. A log offers great protection and minimizes extremes of temperature and dryness. It may be noted also that the two species found are both widespread. It seems that *Camponotus herculeanus pennsylvanicus* can exist wherever large solid logs are found and *Camponotus caryae*, while not a common ant, is also widespread (table I).

In general, species of ants occupying habitats in which there are severe conditions may be divided into two types: those which face their environment and are adjusted to withstand great extremes of heat and dryness, and those which avoid these extremes. The two ants characteristic of the fore dunes are of the latter type. On hot dry days they will be found quietly aggregated several inches below the surface of the sand, emerging only in the cool of the evening, or where the shade keeps the sand surface below the critical temperature.

The nature of sand causes it to hold water to a marked degree. The action of wind on sand causes a dry mulch three to five centimeters thick to be formed (Fuller, '14). This protects the layer beneath, consequently sand

here rarely dries out to the extent and depth of clay or loam and the ants are able to make use of this to exist under conditions which would otherwise be prohibitive.

Poplar dunes.—Behind the fore dunes there is typically a large depression of almost bare sand. Beyond this the poplar dunes rise fifty or more feet on the second series of ridges back from the lake. This ridge is larger than that of the fore dunes and is characterized by scattered clumps of poplars (*Populus deltoides* Marsh). There are also frequent patches of red-osier dogwood (*Cornus stolonifera* Michx.), in addition to the sand cherry, willows, and bunch-grass of the fore dunes.

Conditions of temperature and moisture are essentially those of the fore dunes. Poplars result in a slight addition to the food supply but habitats still consist of bare sand and an occasional log. The instability is still great but there are larger areas of sand held by roots of dogwood and grasses so that the number of *Lasius* and *Pheidole* nests increases greatly. These are again the characteristic ants, with the *Camponotus* group as the only other representative, except an occasional *Formica pallide-fulva schaufussi* which wanders in from the pines.

The way in which ants can avoid extremely high temperatures by going beneath the surface is shown by some of Shelford's ('12) records for the poplar dunes. One summer day when the air temperature was 36° C., that of dry sand 1.25 cm. below the surface was 47° C., while moist sand at that level was only 32° C. At 8 or 9 cm. below the surface moist sand was 29° C. and at 12 or 13 cm. it was 27° C. An ant walking on the surface would have to face a temperature of 47° C. with its accompanying low humidity, while an ant 8 or 9 cm. beneath the surface would face no extremes of heat or dryness. At Whitman Laboratory, on June 10, 1933, it was noted that *Lasius niger neoniger* ants were actively going in and out of craters in the shade while nearby craters in the sun showed no activity. It was found that the sand surface temperature in the sun was 48° C. while eight feet away in the shade the sand surface temperature was only 29° C.

Pine dunes.—Behind the poplars there is usually another smaller depression. From this the more extensive pine dunes rise. Here poplar trees and their accompanying plants have lived and died adding some humus to the sand and binding it with their roots so that a suitable place for pine seedlings is provided. With the pines (*Pinus banksiana* Lamb. and *P. strobus* L.) are found junipers (*Juniperus* sp.), patches of bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), aromatic sumac (*Rhus canadensis* Marsh) and many more of the xeric herbaceous plants. The area has a distinctly evergreen aspect.

Extremes of heat and dryness are cut down to marked degree in the pines. Evaporation is only about half that of the poplar dunes (fig. 1). The slight mixture of humus in the sand seems to be decidedly favorable for several species of ants although the water content of the sand is somewhat less than in

TABLE I. *Ant distribution in the Chicago Area. S = nesting in soil. SL = using soil and log. L = using log*

	Fore Dunes	Poplar Dunes	Pine Dunes	Black Oak on Sand	Red-White Oak on Sand	Mixed Oak on Clay	Oak-Maple on Sand	Beech-Maple Climax	Prairie	Pasture	Stages in Log Succession
1. *Stigmatomma pallipes* Hald.	—	—	—	L	—	L	L	—	—	—	4, 5
2. *Ponera coarctata pennsylvanica* Buck.	—	—	—	L	L	L	L	L	—	S	2, 3, 4, 5, 6
3. *Stenamma brevicorne* Mayr	—	—	—	—	L	L	L	L	—	—	
4. *Aphaenogaster treatae* Forel	—	—	—	S	S	—	—	—	—	—	
5. *Aphaenogaster fulva* Roger	—	—	—	L	—	—	L	L	—	—	4, 5, 6
6. *Aphaenogaster fulva aquia* Buck.	—	—	—	L	L	L	L	L	—	S	3, 4
7. *Aphaenogaster fulva aquia* var. *picea* Emery	—	—	—	—	L	L	L	L	—	—	3, 4, 5, 6
8. *Aphaenogaster tennesseensis* Mayr	—	—	—	—	—	L	L	L	—	—	2, 3
9. *Myrmica punctiventris* Roger	—	—	—	—	—	S	—	—	—	—	
10. *Myrmica scabrinodis brevinodis* var. *sulcinodoides* Emery	—	—	—	—	—	S	S	—	—	—	
11. *Myrmica scabrinodis schencki* var. *emeryana* Forel	—	—	SL	SL	SL	S	S	S	—	—	
12. *Myrmica scabrinodis lobicornis* var. *fracticornis* Emery	—	—	—	—	—	S	—	—	—	S	
13. *Pheidole pilifera* Roger	—	S	—	—	—	—	—	—	—	—	
14. *Pheidole bicarinata* Mayr	S	S	S	S	—	—	—	—	—	—	
15. *Pheidole vinelandica laeviuscula* Emery var.	—	—	S	S	—	—	—	—	—	—	
16. *Crematogaster lineolata* Say	—	—	L	L	—	L	—	—	—	—	2, 3, 4
17. *Crematogaster lineolata* var. *cerasi* Fitch	—	—	—	—	L	L	—	L	—	SL	2, 3, 4
18. *Monomorium minimum* Buck	—	—	S	S	S	—	—	—	—	S	
19. *Monomorium pharaonis* L.	Chicago—hospital and house.										
20. *Solenopsis molesta* Say	—	—	—	SL	SL	S	—	S	S	S	
21. *Myrmecina graminicola americana* Emery	—	—	—	—	—	L	L	L	—	—	4, 5
22. *Leptothorax fortinodis* Mayr	—	—	—	—	—	L	—	—	—	—	
23. *Leptothorax longispinosus* Roger	—	—	—	—	—	L	L	L	—	—	
24. *Leptothorax curvispinosus* Mayr	—	—	—	L	L	L	L	L	—	—	
25. *Leptothorax curvispinosus ambiguus* Emery	—	—	—	—	—	S	—	—	—	S	
26. *Leptothorax texanus* Wheeler	—	—	S	S	—	—	—	—	—	—	
27. *Dolichoderus plagiatus* Mayr	—	—	—	—	—	S	—	—	—	—	
28. *Dolichoderus plagiatus pustulatus* Mayr	Sphagnum bog, Volo, Ill.										
29. *Tapinoma sessile* Say	—	—	—	L	L	L	—	L	—	L	2, 3, 4
30. *Iridomyrmex humilis* Mayr	University of Chicago, Zoology Building										
31. *Iridomyrmex pruinosis* var. *analis* André	—	—	S	—	—	—	—	—	—	—	
32. *Brachymyrmex heeri* var. *depilis* Emery	—	—	—	—	—	S	—	S	—	—	
33. *Camponotus castaneus* Lat.	—	—	SL	SL	—	—	—	—	—	—	
34. *Camponotus castaneus americanus* Mayr	—	—	—	—	—	SL	—	SL	—	—	
35. *Camponotus herculeanus pennsylvanicus* De Geer	L	L	L	L	L	L	L	L	—	L	2, 3, 4
36. *Camponotus herculeanus pennsylvanicus* var. *ferrugineus* Fabr.	—	—	—	—	—	L	—	L	—	L	2, 3, 4
37. *Camponotus herculeanus ligniperdus* var. *noveboracensis* Fitch	—	—	L	L	—	—	—	—	—	—	2, 3, 4
38. *Camponotus caryae* Fitch	L	L	—	—	—	L	L	—	—	L	3
39. *Camponotus caryae* var. *minutus* Emery	—	—	—	L	—	L	—	—	—	—	3
40. *Camponotus caryae subbarbatus* Emery	—	—	—	—	—	—	—	L	—	SL	
41. *Camponotus caryae discolor* Buck.	—	L	—	—	—	L	—	—	—	—	3
42. *Camponotus caryae* var. *tanquaryi* Wheeler	—	—	—	—	—	L	—	—	—	—	

TABLE I (*continued*)

	Fore Dunes	Poplar Dunes	Pine Dunes	Black Oak on Sand	Red-White Oak on Sand	Mixed Oak on Clay	Oak-Maple on Sand	Beech-Maple Climax	Prairie	Pasture	Stages in Log Succession
43. *Paratrechina* (*Nylanderia*) *parvula* Mayr	—	—	S	S	—	—	—	—	—	—	
44. *Paratrechina* (*Nylanderia*) *vividula guatemalensis* Forel	Botany Greenhouse, University of Chicago.										
45. *Prenolepis imparis* Say	—	—	S	S	—	S	—	—	—	—	
46. *Prenolepis imparis* var. near *testacea* Emery	—	—	S	S	—	—	—	—	—	—	
47. *Lasius niger* var. *neoniger* Emery	S	S	S	S	SL	SL	—	—	S	S	2, 3, 4
48. *Lasius niger alienus* var. *americanus* Emery	—	—	—	L	L	L	L	L	S	S	2, 3, 4, 5, 6
49. *Lasius flavus nearcticus* Wheeler	—	—	—	—	L	L	L	L	—	—	4, 5
50. *Lasius umbratus mixtus* var. *aphidicola* Walsh	—	—	—	—	—	L	—	L	—	—	3, 4, 5, 6
51. *Lasius umbratus mixtus* var. *speculiventris* Emery	—	—	—	—	—	—	—	—	—	S	
52. *Lasius* (*Acanthomyops*) *claviger* Roger	—	—	—	—	L	L	—	L	—	—	4
53. *Formica sanguinea aserva* Forel	—	—	—	—	—	S	—	—	—	—	
54. *Formica sanguinea rubicunda* Emery	—	—	—	—	SL	S	—	S	—	S	
55. *Formica sanguinea subintegra* Emery	—	—	—	—	—	S	—	—	—	—	
56. *Formica sanguinea subnuda* Emery	—	—	—	—	—	S	—	—	—	—	
57. *Formica truncicola obscuriventris* Mayr	—	—	—	S	S	—	—	—	—	—	
58. *Formica exsectoides* Forel	—	—	—	—	—	S	—	—	—	S	
59. *Formica ulkei* Emery	—	—	—	—	—	S	—	—	—	—	
60. *Formica fusca* var. *subsericea* Say	—	—	SL	SL	SL	S	S	—	—	S	
61. *Formica fusca* var. *subaenescens* Emery	—	—	—	—	—	SL	SL	SL	—	—	
62. *Formica cinerea* var. *neocinerea* Wheeler	—	—	—	—	—	—	—	—	S	S	
63. *Formica neogagates* Emery	—	—	—	—	—	—	—	—	—	S	
64. *Formica neogagates lasioides* var. *vetula* Wheeler	—	—	—	—	—	—	—	—	—	S	
65. *Formica perpilosa* Wheeler n. var.	University of Chicago campus.										
66. *Formica pallide-fulva schaufussi* Mayr	—	SL	SL	SL	SL	S	—	—	—	S	
67. *Formica pallide-fulva schaufussi* var. *incerta* Emery	—	—	SL	SL	SL	S	—	—	—	S	
68. *Formica pallide-fulva nitidiventris* Emery	—	—	SL	SL	SL	S	—	—	S	S	
69. *Formica pallide-fulva nitidiventris* var. *fuscata* Emery	—	—	—	SL	SL	S	—	—	—	S	
70. *Polyergus rufescens breviceps* Emery	—	—	—	—	—	—	—	—	S	—	
	S, 2 SL, – L, 2	S, 3 SL, 1 L, 3	S, 9 SL, 6 L, 3	S, 10 SL, 8 L, 11	S, 3 SL, 8 L, 11	S, 20 SL, 3 L, 23	S, 3 SL, 1 L, 14	S, 4 SL, 2 L, 18	S, 6 SL, – L, –	S, 19 SL, 2 L, 4	
	4	7	18	29	22	46	18	24	6	25	

the poplars (Fuller, '14). Several habitats are offered: open sand, sand covered with needles or a slight layer of leaves, logs, and even the decayed parts of living trees. Food is more abundant and more varied because of the greater variety of plants and an increase in the number of insects.

Of the eighteen species collected in the pines, nine live in the open sand with no shelter, six require sand with some sort of protection above it (logs, bark, needles) while three are characteristic log-inhabiting forms. Of the species nesting in sand two (*Pheidole bicarinata* and *Iridomyrmex pruinosus analis*) are characteristic of sand and seem confined to it. *Monomorium minimum, Paratrechina (N.) parvula,* and *Lasius niger neoniger* are able to live on bare clay but are more abundant in sand. All of these are eliminated very quickly by a covering of vegetation over the ground, so it would seem that lack of an open substratum is a decided limiting factor in these cases.

An important new element in the pine area is the *Formica pallide-fulva* group. All four of its northern subspecies and varieties are represented. This group and the *Camponotus* members stand out in contrast to the other ants in the pines in that they are adapted to the region in such a way that they meet and withstand extreme environmental conditions. On very hot summer days these two genera are often the only ants seen at the surface—the others are hidden away in the moist sand several inches below the surface.

The southern forms, *Iridomyrmex pruinosus analis* and *Leptothorax texanus* seem almost confined to the pines.

Black oak dunes.—Under the shelter of pines, in the slight humus, and the more moist and moderate conditions, seedling black oaks can start. These gradually crowd out the pine and the pine woods merges into a black oak (*Quercus vetulina* Lam.) associes. With the coming of the oaks minor plants are also crowded out or relegated to the more open places. In their place are found bush honeysuckle (*Diervilla lonicera* Mill), bracken fern (*Pteris aquilina* L.), cactus (*Opuntia rafinesquii* Engelm.), lupine (*Lupinus perennis* L.), and many other shrubs and herbs. Vegetation becomes much more diverse.

In the black oaks, humus has accumulated but the soil is never very thickly covered with leaves and there are many openings which have an essentially pine flora and fauna. Temperature and moisture ranges are not much moderated from those of the pines but plants available for food and shelter have increased greatly.

Of the twenty-nine ants found, only six live in open sand. They are confined to the openings in the oaks and are crowded out where vegetation covers the woods floor. Thus, *Lasius niger neoniger* craters are very abundant in open sand but decayed logs in the deeper woods usually contain nests of *Lasius niger alienus americanus.* The relicts from the pines, *Monomorium minimum, Pheidole bicarinata,* and *Paratrechina (N.) parvula,* are quickly crowded out by leaf covering. *Aphaenogaster treatae* is not common and is usually found nesting at the base of clumps of grass.

The four *Formica pallide-fulva* subspecies and varieties are predominant in the black oaks. Their nests are numerous all through the area and all are constructed on essentially the same plan. They are invariably found under pieces of bark or branches lying lightly on rather open ground. There are one to three holes leading down, and the main chambers of the colony are located ten to fourteen inches deep in the moist, closely packed sand. *Formica pallide-fulva schaufussi* ranges into the more xeric places while *Formica pallide-fulva nitidiventris fuscata* seems the most dependent upon constant moisture conditions.

Many ants not limited to sand invade the black oaks. *Crematogaster lineolata* is very common in rather hard logs in open spots. *Myrmica scabrinodis schenki detritinodis* is frequently found nesting in the sand under sparse leaf covering. *Ponera coarctata pennsylvanica* is found under large logs where the moisture is more constant. *Solenopsis molesta* is not common but is sometimes found in and under twigs and logs. *Tapinoma sessile* will nest under bark, under paper, or in almost any kind of trash. These are all ants which are not confined to moist woods but are often found at woods margins, in fields, or along roads.

Red oak-white oak dunes.—As humus and moisture accumulate the black oaks give way to a red-white associes (*Quercus borealis* Michx. and *Q. alba* L.). There are added many more of the mesic shrubs, vines and herbs such as witchhazel (*Hamamelia virginiana* L.), flowering dogwood (*Cornus florida* L.) and wild lily-of-the-valley (*Maianthemum canadense* Deaf.). This associes differs sharply from the black oaks in that the soil is covered, in almost all places, with a thick layer of leaves and leaf mold.

Formica truncicola obscuriventris is the characteristic ant of this habitat. At times these ants may be very conspicuous when long files are moving brood and fellow workers to a new nest. The nests consist typically of runways which cut into the humus for one half to one inch beneath the heavy leaf covering. They ramify out under the leaves so that one nest may cover four or five square feet of ground.

More mesic conditions are indicated by the coming in of *Stenamma brevicorne, Aphaenogaster fulva aquia picea, Lasius flavus nearcticus* and *Lasius claviger*. Characteristic dunes species are dropping out and consequently the red oak fauna is more like that of the mixed oaks on clay than is the black oak associes. *Aphaenogaster treatae* is the only ant found in the red oaks on sand which has not been found on clay. Since the red oaks on sand have only six species not found in the black oaks and only three not found in oaks on clay it would seem that as a habitat the red oaks are not as distinct as the other two. The relationship of these may be shown by comparing the various oaks (table II). Here "distinct" means that the ant is found in one but not the other of any two habitats compared.

Mixed oak on clay.—On moranic clay the red oak-white oak associes is the most common but in some places there is a mixture of black oak, and in others

TABLE II. *Quantitative distribution of ant species in relation to oak woods and soil*

	Species Distinct			Species Distinct		Species Common to both	
	No.	%		No.	%	No.	%
Black oaks on sand	13	36.1	Red oaks on sand	6	16.7	17	47.2
Black oaks on sand	10	16.9	Oaks on clay	27	48.2	19	33.9
Red oaks on sand	3	6.1	Oaks on clay	26	53.1	20	40.8
All oaks on sand	11	19.6	Oaks on clay	22	39.3	23	41.1

hickories (*Carya* sp.) come in. The environmental conditions and the flora are essentially like the red oak associes on sand but the areas are more widespread and extend over more types of environments. For example, there may be rather dense mesic oak woods and even more moist gullies, or the oaks may form an open, almost pasture-like woods. In these extremes, not only the numbers of colonies of ants differ, but certain species may be able to exist in one and be barred from the other. With this wide diversity of environmental conditions, habitats, and niches, we would expect similar diversity in species. This has proved to be the case; in fact the number of species reaches its climax in the oaks on clay.

In contrast to the few species which depend on the sand substratum and are eliminated by its lack, there seem to be a number of species which depend on clay or clay and loam mixture and cannot penetrate sand. Considering the facts that plants for food and shelter are to a large extent the same, and that moisture and temperature conditions may be similar, it may be that the substratum is a decided limiting factor in keeping a number of ants from entering the dunes. Mound-building ants are excluded except an occasional *Formica fusca subsericea* found nesting under a log. In contrast, the crater-forming *Prenolepis imparis,* typical of yellow clay, may be found occasionally in sand. Moist sand six to twelve inches below the surface will pack to form chambers in much the same manner as clay but a mound of sand would dry out and blow away.

Prenolepis imparis is characteristic of open oak woods on clay and its craters of yellow clay pellets are very common. The ants are active latest in the fall and earliest in the spring of any local species. Chambers are located ten to twelve inches down in solid clay. Here repletes are found in large numbers and winged forms are overwintered, to fly in early spring.

Aphaenogaster tennesseensis is a typical oak woods ant which is rather widespread in its local range but is very much restricted in its nesting site. In all cases colonies have been found either in large fairly hard logs held up off the ground or, more rarely, in the upper parts of large logs lying lightly on the soil. This lack of contact with the soil is characteristic and is all the more interesting in that Wheeler ('10) states that their queen begins her colony in the nest of a variety of *Aphaenogaster fulva,* representatives of which are usually found under logs or stones in much more moist situations.

Species of *Formica* reach their highest diversity in the oaks but are usually found at the edges of woods or in clearings. This is illustrated by the findings concerning a group of 435 *Formica ulkei* mounds at Palos Park. Of these 48 per cent are located along the margin of the woods, 34.3 per cent occur in small open clearings in the interior of the woods, and 17 per cent are located in the open (Dreyer and Park, '32). None occur in dense shade and it seems probable that these ants are able to keep a clearing around their nests by killing sprouting trees and bushes.

Ants depending on leaf secretions and leaf aphids for food reach their greatest abundance in the oaks.

Oak-maple woods on sand.—Only one such transition associes (at Lakeside, Michigan) was studied, but as it gave a rather typical habitat it seemed best to include it separately. Red and white oaks mingle with sugar maple, beech, elm, basswood, and many other species. Hemlock, a remnant from glacial periods, is also present. Five-leafed ivy and wild grape climb into the trees. A lower stratum is composed of dogwood, sassafras, witch-hazel, paw-paw, and red-berried elder. The ground is covered with many kinds of spring flowers. The type of plants indicates that moisture is greater and more constant and that light is limited. The soil is basically sand but a great part of the surface bulk is made up of humus. Leaves cover the ground and many fallen logs are lying in all stages of decay.

Ant colonies are numerous but the number of species is not great. *Aphaenogaster fulva aquia picea* reaches its peak of abundance. It is found under and in almost every thoroughly decayed log lying in a moist situation. The other abundant species are principally those which also require a rather high per cent of moisture: *Stenamma brevicorne, Myrmecina graminicola americana, Lasius flavus nearcticus,* and *Formica fusca subaenescens.*

The niches are leaf covered sand loam, logs in all stages of decay, and living and dead twigs and branches. Ants requiring a solid bare substratum are excluded. In most ways the mixed oak-maple on sand associes is more like the beech-maple climax than the oaks.

Beech-maple association.—This is the climax association toward which all woods on sand or clay are progressing. In the typical beech-maple woods the large old trees give a dense shade. Shrubs are less numerous than in the early woods. Spice bush is typical and paw-paw is limited to the woods edge. In many places bed straw (*Galium alparine* L.) covers the entire floor. This is a vernal plant which by midsummer is reduced to matted stems and innumerable burrs. There are other spring flowers: great white trillium, jack-in-the-pulpit, hepatica, etc. The number of plant species is limited considerably because of lack of light. Moisture is usually constant and abundant, and summer temperature is never extreme. The soil is usually a rich black humus. Leaves cover the ground and large logs are conspicuous. Various niches within the woods may give other habitats. In some places the trees are farther apart and there is more clay in the soil. In others, stream valleys

furnish very moist, well-drained banks. However, there is not the variety of conditions which is found in the oaks.

Under the general substratum conditions, the number of soil-dwelling forms is reduced to a minimum. Most of the species live in logs in some stage of decay, the stage inhabited varying with the species. The number of hypogaeic forms has reached its maximum, whether in response to the reduced light, or because of the increased number of soft, decayed, moist logs, it is impossible to say. Both the number of species and the number of colonies are less than those of the oak woods. This is probably due to the greater constancy of conditions and the lack of variety of habitats. *Lasius niger alienus americanus* and *Aphaenogaster fulva aquia picea* are the only abundant ants in the deep woods. Borders of beech-maple and oak woods are always richest in both species and individuals.

Prairie.—Southwest of Chicago, prairie seems to be the climax plant community instead of forest. Prairies evolve from shallow lakes or marshes, through low prairie characterized by such grasses as *Spartina* and *Calamagrostis*, to climax prairie in which the *Panicum* and *Poa-Andropogon* association is characteristic. Typical plants of the high prairie are the blue stem grasses (*Andropogon* sp.) switch grass (*Panicum virgatum* L.), blue grasses (*Poa* sp.), wild onion (*Allium cernuum* Roth), blazing star (*Liatris spicata* Willd.) and sun flower (*Helianthus* sp.).

In the prairie, ranges of temperature and moisture are as extreme as in the pine dunes. In addition, owing to the nature of the soil, there is apt to be flooding in the spring and more extreme drying out in the summer. Prairie soil is the only habitat and there is little variety in plant food.

The bit of prairie near Chicago is interesting since it is almost a pure *Formica cinerea neocinerea* community. In the high prairie near the Chicago airport, mounds are distributed at no great distance from each other over the entire area. At another location a smaller group of colonies (50 to 75 mounds) is scattered around a marshy pond which dries up in summer. Of the forty-four nests opened, only one was found to contain the slave-making *Polyergus rufescens breviceps*. The *F. cinerea neocinerea* mounds are typically dome-shaped or slightly elongated. The large nests may be twenty-five inches in diameter and from four to six inches high. Occasionally a nest may be found such as one along a ditch slope which was eight feet long and three feet wide. Vigorous nests are usually surrounded by a rim of grass but are entirely bare on top, and have innumerable openings all over the mound.

There are not many other ants which can stand the rigors and lack of habitats of the prairie. *Formica pallide-fulva nitidiventris* and *Lasius niger alienus americanus* are sometimes found.

Succession of Ants in Logs

In the Chicago region there are very few stones, so that ants must rely for their habitats mainly upon soil, or logs, or they may make use of a combination of the two (table I). It will be noted that a large percentage of ants in the beech-maple or oak-maple woods use logs for habitats. This is correlated with two conditions: in the denser woods there are more fallen logs, and the forest floor is not so suitable a habitat as is the more cleared, solid soil of the oaks.

Logs go through characteristic processes of decay, and the characteristic fauna changes with the progressive steps. For convenience the continuous processes of decay has been indicated as representing six stages: *Stage 1.* Tree dead but bark solid; *Stage 2.* Bark loosened, wood solid; *Stage 3.* Sapwood soft, heartwood solid; *Stage 4.* Sap and heartwood soft; *Stage 5.* Beginning to loose shape; *Stage 6.* Merging with the substratum. The distribution of ants through these stages is shown in table I. No ants penetrate into stage one although the *Leptothorax* species may use crevices of solid bark for their nests. Beginning with stage two the widely distributed *Lasius niger alienus americanus* and *Ponera coarctata pennsylvanica* go all the way through. In the harder stages they are found only under the loosened bark. *Aphaenogaster tennesseensis* and the *Camponotus* and *Crematogaster* species seem restricted to rather solid wood. These have their galleries near the surface in hard wood and go deeper as decay progresses. They are not found in the later stages. *Myrmecina graminicola americana* and the yellow *Lasius* species do not come in until the wood is fairly well decayed. Stages three and four reach the climax in both species and numbers. *Aphaenogaster fulva aquia picea* and *Lasius niger alienus americanus* are the most abundant ants in the later stages.

Log succession shows an evolution in miniature where, in general, ants characteristic of more exposed places are found in harder wood and those restricted to more moist conditions live in the more decayed logs. The more widely distributed ants tend to go through a larger series of stages.

Because ants are abundant in every habitat they probably play an important part in the dynamics of succession. The opening up of logs with their galleries so that decay is hastened undoubtedly plays a part in successional changes toward a climax which all woods are approaching. In the early stages of succession ants seem to contribute very little to the hastening of change. In fact, they may retard it by bringing up raw sand or clay to the surface.

Discussion

Table I shows the habitats in which ants have actually been collected. Undoubtedly further collecting would show a larger range on the part of some species. For example, *Stigmatomma pallipes* should occur in the red-white oaks on sand, but since it is a rare ant it has not yet been taken there.

Also, the list is not complete for the area and further collecting should result in the finding of a number of additional species. No indication of abundance of ants is given in the chart. Thus, *Formica fusca subsericea* is listed as occurring all through the sand series as well as on clay and loam. This is true, but the ant is rare on sand while it is one of the most common ants along roadside ditches, and in marshy pastures and woods. For a thorough ecological study of a group, a record of abundance of individuals as well as species is of importance, but this requires special techniques and was not undertaken in this study.

From an ant-distribution viewpoint, the various associes may be designated as ant communities, naming not necessarily the most abundant species, but the ones most restricted to the associes and most characteristic of it.

Fore dunes and poplar dunes: *Pheidole bicarinata* and *Lasius niger neoniger* community.

Pine dunes: *Monomorium minimum* and *Paretrechina* (*N.*) *parvula* community.

Black oak dunes: Community of the *Formica pallide-fulva* subspecies and varieties.

Red-white oak dunes: *Formica truncicola obscuriventris* community.

Mixed oaks on clay: *Prenolepis imparis* and *Leptothorax* spp. community.

Beech-maple climax: *Myrmecina graminicola americana* and *Stenamma brevicorne* community.

Prairie: *Formica cinerea neocinerea* community.

Experiments

Limiting Factors in Distribution

Ants in their distribution, have rather definite and often restricted habitats. The chief factors which may have a general limiting influence are not many. Food, suitable material for a nest, temperature, and moisture seem to be the most important. There may be various other factors such as sunlight, relationship to other ants, etc., which may operate in specific cases. Some ants have a wide range of toleration in regard to each of these, while others are narrowly restricted.

Food is, of course, very important but it is a factor difficult to analyze, because most ants are not restricted to a single type of diet and so may use different foods in different habitats. With ants which depend on aphids for food the relationship to habitat may be secondary, with the toleration of the aphid the limiting factor.

Nesting sites may be specific, or not, depending again on the adaptability of the ant. *Aphaenogaster treatae* and *Iridomyrmex pruinosus analis* seem entirely confined to a sand substratum. Ant mounds are excluded from the dunes. Some of the genus *Camponotus* seem confined to logs. Species

of *Crematogaster* are found in logs where they are available, but will also nest under stones. *Lasius niger alienus americanus* will nest equally readily in logs, under stones, or in soil.

Sunshine may perhaps be a direct factor (Dreyer and Park, '32) in preventing some species from nesting in deep woods, or it may have a secondary effect in that, with lack of sunshine, moisture becomes too great.

Absence of certain other ants is a limiting factor in the case of slavemakers. Thus, since *Polyergus rufescens breviceps* ants must have other species to care for them, they are restricted to places where the slave ants are abundant. The number of slave-maker individuals is also restricted, in that they must be far less abundant in a region than their slaves.

Temperature and moisture seem the most important limiting factors for ants in general. Moisture is probably more important (if the two can be truly separated). Shelford ('13a) says, "A comparison of Fuller's (fig. 1) data with the tables or lists of animals shows that the distribution and succession of animals is clearly correlated with the evaporating power of air." Again he states, "From the standpoint of including many factors, the evaporating power of the air is by far the most inclusive and is therefore by far the best index of physical conditions surrounding animals wholly or partly exposed to the atmosphere."

Assuming that moisture is very important in ant distribution, the problem was set to see whether there were differences in toleration among various species to extremely dry conditions, and whether these differences could be correlated with distribution. In most of the experimental work, *Formica* species were used because these ants meet and withstand extremes of heat and dryness in contrast to other species which stay underground and so avoid the extremes.

Ants were easily kept in good condition in the laboratory by putting them, together with soil of their nests, in large pans with rims of Arctic cup grease around the tops. They were fed on honey and liver with occasional feedings of various kinds of fruits and meats.

Apparatus and Technique

In testing the ants they were subjected to a slow flow of air of specified dryness and temperature. They were kept in these conditions until death occurred.

The apparatus used in testing toleration of various species to low relative humidity at fixed temperatures was similar to that which Pearson ('33) figures and describes. It is placed in a water bath which regulates the temperature. Compressed air is bubbled slowly (two to five liters per minute) through distilled water, then through concentrated sulphuric acid which takes out most of the moisture. From here it is led through a jar containing activated charcoal and glass wool to remove any fumes which might be present,

and then through a bottle of calcium chloride for a final drying before it is led to the jar containing the ants. When higher humidity is desired a stopcock is loosened which allows the dry air to be mixed with that passed through distilled water. The bottle containing the ants is a two liter museum jar sealed with vacuum wax. Within it is placed a hair hygrometer which records temperature as well as relative humidity. Each ant is placed in a separate glass tube 60 mm. long, and with an inside diameter of 8 mm. This gives the ant sufficient space to move about. The two ends are covered with copper mesh which allows a free diffusion of air through the tube. The tubes are strung together and are hung on the back of the hygrometer. Four sets of seven, or twenty-eight such tubes can be included in a jar at one time. Usually two complete experiments of this type were run simultaneously in the water bath and all data from both were combined. The hair hygrometers were checked before each experiment with a wet and dry bulb sling psychrometer.

The ants were placed in the tubes one at a time. Very few were injured by this handling but all the ants were checked before each set was put into the jar. Observations were made every half hour, hour, or three hours according to the length of time of the experiment. Readings were made by taking the jars out of the water bath and looking through the tubes with a reading glass toward an electric light. The jars were never out of the water bath for more than three or four minutes at a time and the temperature deviated very little during that period. Each jar always contained equal numbers of all species tested.

Ants have a characteristic manner of dying. After running about for a time they fall forward, or on one side, and begin twitching their legs. This twitching gradually becomes more feeble until at last it ceases. Immobility—not death—is taken as the end point since there is no way of determining just when death occurs. Ants taken out soon after they have ceased motion can sometimes move their legs slightly, but they do not recover.

Formica Species Used and Their Distribution

For most of the experiments six species of the genus *Formica* were used: (1) *Formica truncicola obscuriventris* seems almost confined to the oak dunes, and there forms nests of anastomosing runways just under the leaf covering; (2) *F. pallide-fulva schaufussi incerta* is also a very common ant at the oak dunes, nesting under bark or logs and having chambers extending down into the sand. It is also found in rather open clay at the borders of fields or in clearings of oak woods; (3) *F. cinerea neocinerea* occurs all through the prairie region, by roadside ditches, around small ponds, and also in the flat dry high prairie; (4) *F. fusca subsericea* is common along roads, at woods edges, or in low marshy fields. The nests always seem to be located where ground water is accessible; (5) *F. sanguinea rubicunda* is not common

but has been found with *F. fusca subsericea* along road ditches or at the edge of oak woods; (6) *F. ulkei* is found at only one place and here the numerous nests are scattered around a shallow pond in an oak woods clearing.

In general, ants 1, 2 and 3 are present in places where fluctuations of temperature and moisture are very great and often severe, while 4, 5 and 6 nest in places where there is a rather constant moisture supply. These environmental differences are indicated in Fuller's table of comparative mean daily evaporation (fig. 1).

Experimental Results

Formica species compared.—The ants were tested with regard to three degrees of severity of dryness and high temperature (table III).

TABLE III. *Average survival time of ants at three degrees of low humidity and high temperature*

Ants	16 ants 30.6 ± .3° C. 12.1 ± 2.7% r. h. Hours Survived	18 ants 34.4 ± .5° C. 9.2 ± 1.5% r. h. Hours Survived	16 ants 41.2 ± .8° C. 8.3 ± .1% r. h. Hours Survived
F. obscuriventris	14.06	10.00	1.93
F. neocinerea	9.50	6.22	1.57
F. incerta	8.12	8.00	1.43
F. rubicunda	6.62	4.94	1.04
F. ulkei	6.18	3.61	.84
F. subsericea	2.81	3.61	.92

Table IV gives these data in full with the duplicate experiments checking the results. It also gives a comparison of each species with every other species and the significance of the difference in survival time between each two as worked out by Student's ('25) method of analysis. By this method, a significance of .0500 means that there are five chances in one hundred of the results being obtained by chance. A figure of .0100 means that there is only one chance in one hundred of random sampling giving the same result. In this work it is considered that a number of .0100 or less indicates that some other factor than chance is responsible for the difference in length of life of any two species. Any figure from this up to .0500 is of border-line significance.

Table V gives significance of the data of experiments 1, 2, and 3 (table IV) and compares each ant with every other ant. Underlining indicates that the difference is considered significant. Where there is not an underlining chance may be responsible for the difference in survival time.

It will be seen from these three tables that *F. truncicola obscuriventris, F. pallide-fulva schaufussi incerta,* and *F. cinerea neocinerea* are definitely able to stand dryness at high temperatures for a longer time than the other three species. This checks very nicely with their distribution as pointed out in an earlier paragraph, i.e., these three species are found in open dunes, fields, or

TABLE IV. *Survival times and significance correlations of ants subjected to dry conditions at high temperatures*

Formica		1. 30.6 ± .3° C. 12.1 ± 2.7% relative humidity 16 ants				1a. 30.1 ± .3° C. 13.2 ± 2.2% relative humidity 15 ants			
a	*b*	hr.a.[1]	hr.b.[1]	diff.	sig.	hr.a.[1]	hr.b.[1]	diff.	sig.
F. obscuriventris	*F. neocinerea*	14.06	9.50	4.56	.0104	—	—	—	—
F. "	*F. incerta*	14.06	8.12	5.94	.0142	—	—	—	—
F. "	*F. rubicunda*	14.06	6.62	7.44	.0000	—	—	—	—
F. "	*F. ulkei*	14.06	6.18	7.88	.0004	—	—	—	—
F. "	*F. subsericea*	14.06	2.81	11.25	.0000	—	—	—	—
F. neocinerea	*F. incerta*	9.50	8.12	1.38	.3824	8.80	6.80	2.00	.1778
F. "	*F. rubicunda*	9.50	6.62	2.88	.0432	8.80	6.06	2.74	.0414
F. "	*F. ulkei*	9.50	6.18	3.32	.0512	8.80	6.86	1.94	.2218
F. "	*F. subsericea*	9.50	2.81	6.69	.0002	8.80	2.53	6.27	.0056
F. incerta	*F. rubicunda*	8.12	6.62	1.50	.1472	6.80	6.06	.74	.4546
F. "	*F. ulkei*	8.12	6.18	1.94	.0938	6.80	6.86	.06	.5916
F. "	*F. subsericea*	8.12	2.81	5.31	.0002	6.80	2.53	4.27	.0000
F. rubicunda	*F. ulkei*	6.62	6.18	.44	.7986	6.06	6.86	.80	.5714
F. "	*F. subsericea*	6.62	2.81	3.81	.0000	6.06	2.53	3.53	.0000
F. ulkei	*F. subsericea*	6.18	2.81	3.37	.0004	6.86	2.53	4.33	.0016

Formica		2. 34.2 ± .5° C. 9.2 ± 1.5% relative humidity 18 ants				2a. 35.3 ± .8° C. 11.0 ± 2.2% relative humidity 16 ants			
a	*b*	hr.a.[1]	hr.b.[1]	diff.	sig.	hr.a.[1]	hr.b.[1]	diff.	sig.
F. obscuriventris	*F. neocinerea*	10.00	6.22	3.78	.0048	—	—	—	—
F. "	*F. incerta*	10.00	8.00	2.00	.1858	—	—	—	—
F. "	*F. rubicunda*	10.00	4.94	5.06	.0004	—	—	—	—
F. "	*F. ulkei*	10.00	3.61	6.39	.0000	—	—	—	—
F. "	*F. subsericea*	10.00	3.61	6.39	.0000	—	—	—	—
F. neocinerea	*F. incerta*	6.22	8.00	1.78	.1332	—	—	—	—
F. "	*F. rubicunda*	6.22	4.94	1.28	.1624	—	—	—	—
F. "	*F. ulkei*	6.22	3.61	2.61	.0034	—	—	—	—
F. "	*F. subsericea*	6.22	3.61	2.61	.0048	—	—	—	—
F. incerta	*F. rubicunda*	8.00	4.94	3.06	.0006	—	—	—	—
F. "	*F. ulkei*	8.00	3.61	4.39	.0008	6.68	4.00	2.68	.0026
F. "	*F. subsericea*	8.00	3.61	4.39	.0000	6.68	3.00	3.68	.0000
F. rubicunda	*F. ulkei*	4.94	3.61	1.33	.0670	—	—	—	—
F. "	*F. subsericea*	4.94	3.61	1.29	.0014	—	—	—	—
F. ulkei	*F. subsericea*	3.61	3.61	0.00	1.0000	4.00	3.00	1.00	.1544

Formica		3. 41.2 ± .8° C. 8.3 ± 1.1% relative humidity 16 ants				3a. 40.7 ± .3° C. 13.5 ± 1.4% relative humidity 12 ants			
a	*b*	hr.a.[1]	hr.b.[1]	diff.	sig.	hr.a.[1]	hr.b.[1]	diff.	sig.
F. obscuriventris	*F. neocinerea*	1.93	1.57	.36	.0962	—	—	—	—
F. "	*F. incerta*	1.93	1.43	.50	.0800	—	—	—	—
F. "	*F. rubicunda*	1.93	1.04	.89	.0016	—	—	—	—
F. "	*F. ulkei*	1.93	.84	1.09	.0000	—	—	—	—
F. "	*F. subsericea*	1.93.	.92	1.01	.0004	—	—	—	—
F. neocinerea	*F. incerta*	1.57	1.43	.14	.3766	2.79	1.60	1.19	.0070
F. "	*F. rubicunda*	1.57	1.04	.53	.0038	2.79	1.20	1.59	.0124
F. "	*F. ulkei*	1.57	.84	.73	.0030	2.79	.95	1.84	.0104
F. "	*F. subsericea*	1.57	.92	.65	.0016	2.79	.83	1.96	.0000
F. incerta	*F. rubicunda*	1.43	1.04	.39	.0088	1.60	1.20	.40	.0840
F. "	*F. ulkei*	1.43	.84	.59	.0094	1.60	.95	.65	.0262
F. "	*F. subsericea*	1.43	.92	.51	.0028	1.60	.83	.77	.0262
F. rubicunda	*F. ulkei*	1.04	.84	.20	.2688	1.20	.95	.25	.0954
F. "	*F. subsericea*	1.04	.92	.12	.2932	1.20	.83	.37	.0392
F. ulkei	*F. subsericea*	.84	.92	.08	.5260	.95	.83	.12	.6072

[1] Hr.a. refers to average survival time of ants of column a. (Example: at 30.6° C. and 12.1 per cent relative humidity the average survival time of *F. obscuriventris* was 14.06 hours.) Hr.b. gives similar results for column b.

TABLE V. *Showing significances of differences in survival times*[1]

Formica		30.6° C. 12.1% rel. humid.	34.2° C. 9.2% rel. humid.	41.2° C. 8.3% rel. humid.
F. obscuriventris	*F. incerta*	.0142	.1858	.0800
F. "	*F. neocinerea*	.0104	.0048	.0962
F. "	*F. rubicunda*	.0000	.0004	.0016
F. "	*F. ulkei*	.0004	.0000	.0000
F. "	*F. subsericea*	.0000	.0000	.0004
F. incerta	*F. obscuriventris*	.0142	.1858	.0800
F. "	*F. neocinerea*	.3824	.1332	.3766
F. "	*F. rubicunda*	.1472	.0006	.0088
F. "	*F. ulkei*	.0938	.0008	.0094
F. "	*F. subsericea*	.0002	.0000	.0028
F. neocinerea	*F. obscuriventris*	.0104	.0048	.0962
F. "	*F. incerta*	.3824	.1332	.3766
F. "	*F. rubicunda*	.0432	.1624	.0038
F. "	*F. ulkei*	.0512	.0034	.0030
F. "	*F. subsericea*	.0002	.0048	.0016
F. rubicunda	*F. obscuriventris*	.0000	.0004	.0016
F. "	*F. incerta*	.1472	.0006	.0088
F. "	*F. neocinerea*	.0432	.1624	.0038
F. "	*F. ulkei*	.7986	.0670	.2688
F. "	*F. subsericea*	.0000	.0014	.2932
F. ulkei	*F. obscuriventris*	.0004	.0000	.0000
F. "	*F. incerta*	.0938	.0008	.0094
F. "	*F. neocinerea*	.0512	.0034	.0030
F. "	*F. rubicunda*	.7986	.0670	.2688
F. "	*F. subsericea*	.0004	1.0000	.5260
F. subsericea	*F. obscuriventris*	.0000	.0000	.0004
F. "	*F. incerta*	.0002	.0000	.0028
F. "	*F. neocinerea*	.0002	.0048	.0016
F. "	*F. rubicunda*	.0000	.0014	.2932
F. "	*F. ulkei*	.0004	1.0000	.5260

[1] Numbers underlined are considered to indicate significant differences. For actual survival times in hours consult table IV.

prairie where during the summer drought is often severe, while *F. fusca subsericea*, *F. sanguinea rubicunda*, and *F. ulkei* occur in places where the water supply is more constant.

Since both relative humidity and temperature were changed for each experiment there was a question whether perhaps temperature and not moisture was the controlling factor. To answer this question a series of experiments was run at 30.4° C. (the same as in experiment 1, table IV) with a higher relative humidity (44.3 per cent).

Table VI shows the results of three combined experiments using forty-two ants of each species. Only four species were available.

TABLE VI. *Average survival time of ants at designated temperature and relative humidity*[1]

		30.4 ± .34° C. and 44.3 ± 1.2% rel. hum. Hours Survived	Hours Survived	Diff.	Sig.
F. incerta	*F. subsericea*	54.49	41.64	12.95	.6912
F. incerta	*F. neocinerea*	54.49	25.35	29.14	.0000
F. incerta	*F. ulkei*	54.49	18.16	36.43	.0000
F. subsericea	*F. neocinerea*	41.64	25.35	16.29	.1224
F. subsericea	*F. ulkei*	41.64	18.16	23.48	.0248
F. neocinerea	*F. ulkei*	25.35	18.16	7.19	.1952

[1] The first column marked "hours survived" refers to the length of life of ants of the first column (thus *F. incerta* lived 54.49 hours) while the second column of figures records survival time of the second column of ants (thus *F. subsericea* averaged 41.64 hours of life).

It will be noted that the ants lived enormously longer at high humidity, and what is more interesting, the relationships between the different species as to length of life changed. *F. fusca subsericea*, which died first under the very dry conditions, lived almost as long as did *F. pallide-fulva schaufussi incerta*, and considerably longer than *F. ulkei*.

Other results not yet fully checked indicate that at the same temperature and still higher relative humidity (70 per cent) *F. fusca subsericea* lives slightly longer than *F. cinerea neocinerea* and *F. ulkei*. Of these, *F. cinerea neocinerea* dies first. Thus, the relationships of the species is just reversed at low and high humidities.

Thus it would seem evident that the ants died differentially in the first experiments as a result of their differences in ability to tolerate low relative humidity and not in response to high temperature. This is at least true at 30° C. and since the relationships are consistent at 30°, 34° and 41° C. it is assumed that at even these higher temperatures the ants died sooner because of dryness.

Other species compared.—The same type of experiment was tried with several other kinds of ants.

(*a*) *Aphaenogaster fulva aquia* is rather common along road and railroad ditches or in open oak woods. Its variety, *A. picea*, occurs in beech-maple woods and especially along moist stream gullies of these woods. These two ants were compared (table VII) because their differences in distribution seem influenced by different moisture optimums. There seems no doubt that there is a definite physiological difference between these two ants with reference to their ability to withstand dryness, and that this difference is correlated with their distribution.

TABLE VII. *Average survival time of Aphaenogaster varieties*

		A. aquia Hours Survived	*A. picea* Hours Survived	Diff.	Sig.
I	21 ants 30.3 ± .2° C. 12.3 ± 1.8% rel. hum.	5.88	3.85	2.03	.0002
II	21 ants 30.0 ± .2° C. 11.5 ± 3.0% rel. hum.	9.97	4.88	5.09	.0000

Comparing *Lasius* species the results are quite different.

(*b*) *Lasius niger neoniger* is most common on the exposed dunes and *Lasius niger alienus americanus* is abundant in deep moist woods, yet their ranges overlap and both are also found in dry pastures which may show as definite lack of water as the dunes. There is no evidence (table VIII) that there is a differential in the toleration of these ants, although the second experiment shows a borderline significance toward *L. americanus* as being the more tolerant of the two. It would seem that the difference in distribution of the two is not a response to dryness. It is interesting to remember in this case that *Lasius niger* varieties do not come out in hot dry weather so they do not face severe conditions.

TABLE VIII. *Average survival time of Lasius subspecies*

		L. neoniger Hours Survived	*L. americanus* Hours Survived	Diff.	Sig.
I	19 ants 30.1 ± .4° C. 17.8 ± 3.3% rel. hum.	4.76	4.37	.19	.8056
II	19 ants 22.7 ± .9° C. 16.7 ± .9% rel. hum.	4.02	5.94	1.92	.0474

(*c*) *Lasius niger alienus americanus* was tested against *L. umbratus mixtus aphidicola*, a hypogoeic species which usually lives in logs in oak and beech-maple woods. In this case also there is no sign of a differential in respect to toleration of low relative humidity.

(*d*) It was found that *Camponotus herculeanus pennsylvanicus* is unique in that it ranges from the most exposed poplar dunes to moist stream valleys in beech-maple woods. Nests of this species were collected and tested from a very moist situation and a very dry one (table IX). There is no indication in this case that the habitat of an individual nest makes a difference in dry toleration within a species.

TABLE IX. *Average survival time of Camponotus herculeanus pennsylvanicus from different habitats*

C. pennsylvanicus	Moist Situation Hours Survived	Dry Situation Hours Survived	Diff.	Sig.
21 ants 30.2 ± .2° C. 12.1 ± 3.0% rel. hum.	44.19	39.47	4.72	.4920

(*e*) The question arose as to whether keeping ants in the laboratory might make some difference in their toleration. In a test with *Formica ulkei* there is no evidence that keeping these ants in the laboratory over winter makes any difference in their reaction to dryness. Neither do ants from different mounds show significant variation.

It seemed interesting to test whether the different castes of a colony would show differential toleration. Experiments testing this were tried with several species.

(*f*) *Camponotus herculeanus pennsylvanicus,* female, worker, and male were tested (table X). It is clear from these two tests that the females are much more resistant than are the workers, and these are in turn more hardy than the males. At higher temperatures the workers begin to loose their superiority to the males. The female is still much more resistant.

TABLE X. *Average survival time of different castes of Camponotus*

Hours Survived	Hours Survived	Difference	Significance
14 ants 30.0 ± .5° C. 12.8 ± 2.4% rel. hum.			
♂—21.35	♀—90.14	68.79	.0000
☿—48.14	♀—90.14	42.00	.0000
♂—21.35	☿—48.14	26.79	.0040
14 ants 30.3 ± .6° C. 11.5 ± 2.5% rel. hum.			
Hours Survived	Hours Survived	Difference	Significance
♂—20.71	♀—74.50	53.79	.0000
☿—44.21	♀—74.50	30.29	.0002
♂—20.71	☿—44.21	23.50	.0016

(*g*) *Lasius umbratus mixtus aphidicola,* female, worker, and male were tested. This experiment was run three times (table XI). The females had superior resistance but the results comparing the males and workers were inconclusive.

TABLE XI. *Average survival time of females, workers and males of Lasius*

		Hours Survived	Hours Survived	Diff.	Sig.
I	15 ants 30.2 ± .3° C. 12.1 ± 2.3% rel. hum.	♂—3.90	♀—8.30	4.40	.0000
		☿—3.63	♀—8.30	4.67	.0000
		♂—3.90	☿—3.63	.27	.4488
II	15 ants 30.3 ± .2° C. 13.8 ± 2.3% rel. hum.	♂—4.66	♀—7.90	3.24	.0000
		☿—3.06	♀—7.90	4.84	.0000
		♂—4.66	☿—3.06	1.60	.0086
III	16 ants 30.2 ± .3° C. 13.0 ± 3.9% rel. hum.	♂—5.40	♀—8.53	3.13	.0000
		☿—4.46	♀—8.53	4.07	.0000
		♂—5.40	☿—4.46	.94	.0652

(*h*) *Formica fusca subaenescens* females were tested against the workers of the colony and *Aphaenogaster tennesseensis* females were tested against their workers. In both cases there are again significant differences in favor of the females.

From these tests there is no doubt of the superior resistance of the female, but the results comparing the male and workers are not conclusive. Whether the survival is due to the larger size of the female is not determined. Whatever the cause, there is undoubted survival value for the colony as well as for the female herself. The relationship between the male and workers seems to vary with different species, perhaps in correlation with size differences between the two.

Among the *Formica* species differences in size cannot account for differences in toleration. While the size differences are not great, *F. neocinerea* is a smaller ant than either *F. ulkei* or *F. subsericea.* Nevertheless, under very dry conditions, it lives significantly longer than either of these.

Discussion

Few papers have been found which deal with physiological differences between species of a genus which can be correlated with niches occupied. However, the following three illustrate this type of work.

Parker ('30) worked out the optimum developmental temperatures for three species of grasshoppers of the genus *Melanoplus.* He found that *M. femur-rubrum* had a lower optimum than did *M. mexicanus* or *M. packardi.* Concerning their distribution Parker states, "This species (*M. femur-rubrum*) is most commonly found in bushy areas along streams or in rank-growing grass, while the other species prefer unshaded ground, sparsely covered with vegetation, and are thus adapted to a higher range of temperature."

Shelford ('13b) subjected two salamanders of the genus *Plethodon* to a humidity gradient and found that *P. glutinosus* is more sensitive to dry air than is *P. cinereus.* This is definitely correlated with habitat differences as *P. glutinosus* lives in damper places than does *P. cinereus.* The results are especially interesting in that *P. cinereus* is the smaller animal and its evaporating surface per unit weight would be greater for that reason.

Williams ('34) experimented with two species of termites, *Reticulitermes hesperus,* characteristic of more moist regions, and *R. tibialis* of more arid places. He found that *R. tibialis* could live with slightly less moisture in the soil than could *R. hesperus.* He also discovered that *R. hesperus* could tolerate a greater amount of carbon dioxide which is correlated with high moisture content. He says, "Thus both low and high soil moisture contents appear to serve as controlling factors in the distribution of these two subterranean termites."

It is established in the preceding pages that there are definite physiological

differences between *Formica* species living in dryer situations and those inhabiting more moist places. In general, differences between species are usually considered nonadaptive, and are explained on the basis of isolating factors, but in these cases the physiological differences appear definitely adaptive in that they are correlated with the type of habitat which the animal can utilize.

Summary

1. Seventy species, subspecies, and varieties of ants were collected within a radius of ninety miles of Chicago.

2. Records were kept showing their distribution through the following ecological stages: (*a*) beach; (*b*) fore dunes; (*c*) poplar dunes; (*d*) pine dunes; (*e*) black oak dunes; (*f*) red-white oak dunes; (*g*) mixed oak woods on clay; (*h*) oak-maple woods on sand; (*i*) beech-maple climax; and (*j*) prairie.

3. It was found that species reached their peak of abundance in the oaks on clay. This was correlated with diversity of habitats in that associes, and with lack of extreme temperature or dryness.

4. Few species are restricted to sand although some are much more abundant there. In contrast, sand seems a limiting factor in many species.

5. A definite succession of species through stages in decaying logs was found. This correlates in a broad way with general distribution of the ants, those of the less exposed places being restricted to the later stages of decay.

6. From distribution studies it seemed probable that toleration or lack of toleration to extremes of dryness is one of the important differentiating factors in the distribution of species, allowing some forms to penetrate into places of low relative humidity where others are excluded.

7. To test this observation experimentally six species of the genus *Formica* were subjected to controlled conditions of dryness. It was found that those living in the drier places (black oak dunes, prairie, etc.) were more resistant to dryness than those living where the moisture supply is more constant.

8. For species of *Lasius* no such differentiation to dryness could be found. These ants do not forage on hot dry days and so do not face extremes to the extent that the *Formica* ants do.

9. In all cases tested females lived much longer under dry conditions than did workers or males of the same colony. This may be due to superior size. In any case it should be of survival value to the colony in that the isolated female may be subjected to severe conditions when founding her colony.

10. Variations in the survival times among various species of *Formica* demonstrate physiological differences between the species living in moist places and those of dryer situations. These differences are probably adaptive in that they are correlated with the ability of the species to penetrate niches where the moisture supply may be very low at times.

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TEMPERATURE RELATIONS OF THE BUNCHBERRY, *CORNUS CANADENSIS* L.[1]

EDGAR T. WHERRY

University of Pennsylvania

The significance of temperature in restricting the migration of plants northward is widely recognized, and those which exhibit an ability to withstand frost are classed as "hardy." That temperature may also limit the movement of northern species southward is less generally appreciated, and there appears to be no term in common use to characterize plants unable to withstand hot summer conditions. The technical term "thermophobic" is rather too cumbersome for popular favor, although it may be more acceptable if shortened to "thobic." As several presumably thobic plants reach their southern limits in fairly accessible portions of Pennsylvania or neighboring states, a study of the relation of their distribution to temperature seemed worth undertaking. A fund awarded to the writer by the Board of Graduate Education and Research of the University of Pennsylvania for ecological investigation has accordingly been used to partially defray the expenses of field trips to significant localities, and to have analyses for certain soil constituents made.[2]

As the subject for study the bunchberry, *Cornus canadensis* L., was selected. This is a common under-shrub of woods, bogs, and barrens from eastern Asia and Alaska to Labrador and Newfoundland, and down to the northern borders of the United States. Further south it becomes sporadic or rare, and reaches its southernmost limits, so far as known, at about latitude 38° 35′ in the higher Appalachians. Its relations to temperature and soil nitrogen have been examined at several localities from Syracuse, New York, to Cheat Bridge, West Virginia, and the results will be presented here in this sequence.

New York. According to House ('24) the bunchberry is "common across the state northward. Locally common westward to Lake Erie, and southward to Columbia, Ulster and Delaware counties. Formerly on Long Island." In parts of the State where there are extensive limestone outcrops it is, however, rare, and around Syracuse it seems to occur only in certain peculiar depressions of glacial origin, as described by Petry ('18). On September 5, 1932, several of these depressions lying one to two miles east of

[1] Contribution from the Botanical Laboratory and Morris Arboretum of the University of Pennsylvania.

[2] The analytical work has been carried out by Mr. Horace J. Hallowell, consulting chemist of Philadelphia.

Jamesville were visited, and the relations of the plants studied. In the cooler parts of the basins the limestone blocks were found to be covered by a layer of brown, fibrous humus 1 to 10 cm. thick, in which were rooted extensive colonies of the northern species, *Cornus canadensis, Linnaea borealis, Coptis trifolia* and *Ribes lacustre.* A sample of this soil was collected for analysis at a point where the *Ribes* was dominant, but the *Cornus* was present at least marginally. For comparison another sample was obtained about 15 meters up the slope of the basin, where black powdery humus covered the rock fragments and supported a nearly pure stand of the fern, *Cystopteris bulbifera.* The samples were transported in glass jars, a few cc. of toluene being added to each to prevent the activities of organisms, and analyzed for nitrogen by official methods. The results of observations and analyses on these are shown in table I.

TABLE I. *Data on soils in depression in limestone, near Jamesville, New York*

	Cystopteris	*Ribes-Cornus*
Air temperature	85° F. (29.5° C.)	75° F. (24° C.)
Soil temperature, 1 cm. depth	75° F. (24° C.)	60° F. (15.5° C.)
Soil temperature, 10 cm. depth	72° F. (22° C.)	56° F. (13.5° C.)
Total nitrogen	2.23 per cent	1.73 per cent
Nitrogen in ammonia form	0.067 per cent	0.036 per cent
Nitrogen in nitrate form	0.0004 per cent	0.0003 per cent
Active acidity or alkalinity	alk. (2 pH 7.5)	ac. 100 (pH 5.0)

The data in table I show that the cool temperature of the bottom of the depression favors the development in the humus of a high degree of acidity. Neither temperature nor acidity is able to prevent the activities of nitrifying organisms, however, ¾ as much nitrate being present in the cold as in the warm soil at this locality.

New Jersey. Cornus canadensis is recorded from five counties in this state—Hudson, Mercer, Morris, Sussex, and Warren—at elevations ranging from 1500 feet down to sea level. No temperature measurements have been made here, but at one locality, Green Pond, lying at an altitude of 400 feet in the last-named county, the peat in which it grows is sensibly cooler than the soils of nearby hills, owing to the uprising of cold spring water.

Pennsylvania. The county list for *Cornus* in this state is: Berks, Carbon, Center, Clinton, Erie, Huntingdon, Lehigh, Luzerne, Mifflin, Monroe, Pike, Schuylkill, Somerset, Sullivan, and Tioga. Most of these lie at rather high altitudes toward the central and northern parts of the state, where the climate and soils are relatively cool. Observations were made upon it at its southernmost known occurrence within the state, on Negro Mountain, ¼ mile west of the fire tower shown on the Meyersdale topographic sheet, 6 miles northwest of Salisbury, Somerset County, at 3175 feet altitude. On the thinly wooded plateau humus has accumulated to depths of 5 to 25 cm. in hollows between quartzite rock fragments, and its acidity is uniformly high. This humus supports extensive colonies of mosses, chiefly *Polytrichum* sp. in

the dryer and *Sphagnum* sp. in the more moist places. The rootstocks of the *Cornus* extend through the moss carpets at depths of 2 or 3 centimeters. Because of the high elevation the temperature of the soil remains low throughout the summer; the results of measurements made at about the warmest period—August 6, 1933—are presented in table II, below.

Maryland. So far as known bunchberry is found in this state only in the higher mountains of Garrett County. There is no reason to suppose that its relations would be different from those in the nearby Pennsylvania localities.

West Virginia. At the time of compilation of Millspaugh's ('13, p. 320) catalogue of the plants of the state only two localitities were known—Ice Mountain in Hampshire County and Spruce Knob in Pendleton, the highest point in the state, altitude 4860 feet. In his list of trees and shrubs Brooks ('20) added one more locality—Osceola, Randolph County, altitude 3500 feet. On July 19, 1933, the writer made observations on a colony of it, also lying in Randolph County, but somewhat further southwest, namely, in the extensive swamp 1½ miles southeast of Cheat Bridge, at an altitude of 3650 feet. This swamp is of interest in supporting a forest of balsam fir trees, the species of which was given by Millspaugh as *Abies balsamea,* and by Brooks as *Abies fraseri,* but which proved on close examination to represent the apparent intermediate between these named by Fernald *Abies balsamea* var. *phanerolepis.* The data obtained here are shown in comparison with those at the above-mentioned station in Somerset County, Pennsylvania, in table II.

TABLE II. *Data on soils of Cornus canadensis in Pennsylvania and West Virginia*

	Fire Tower, Somerset Co., Pa.	Cheat Bridge, Randolph Co., W. Va.
Air temperature	75° F. (24° C.)	75° F. (24° C.)
Soil temperature, 3 cm. depth	63° F. (17° C.)	62° F. (16.5° C.)
Soil temperature, 10 cm. depth	59° F. (15° C.)	57° F. (14° C.)
Total nitrogen	0.73 per cent	1.05 per cent
Nitrogen in ammonia form	0.004 per cent	0.035 per cent
Nitrogen in nitrate form	0.0002 per cent	0.0004 per cent
Active acidity	315 (pH 4.5)	315 (pH 4.5)

The acidity is greater than at the New York locality studied, yet even here the formation of nitrate in the soil goes on to some extent.

The locality known as Ice Mountain is situated in Hampshire County, toward the eastern side of the state, at an altitude of only 775 feet. Ordinarily northern plants would not be expected to occur at such a low elevation this far south, but here, because of the peculiar configuration of the rock slopes and talus heaps the ice which accumulates during the winter fails to melt until late in the summer, so that the rocks are kept continuously cool. A considerable thickness of acid humus has accumulated, and in it grow *Cornus canadensis, Linnaea borealis,* and *Ribes prostratum.* Data obtained here on August 5th, 1932, are presented in table III.

TABLE III. *Data on soils at Ice Mountain, West Virginia*

	Cornus canadensis	*Betula lenta*
Air temperature	80° F. (26.5° C.)	80° F. (26.5° C.)
Soil temperature, 3 cm. depth	57° F. (14° C.)	70° F. (21° C.)
Soil temperature, 10 cm. depth	51° F. (10.5° C.)	68° F. (20° C.)
Total nitrogen	1.02 per cent	0.49 per cent
Nitrogen in ammonia form	0.028 per cent	0.012 per cent
Nitrogen in nitrate form	0.0004 per cent	0.0003 per cent
Active acidity	315 (pH 4.5)	100 (pH 5.0)

In explanation of the low nitrogen content of the warmer *Betula lenta* soil, it should be noted that this was relatively high in mineral matter and correspondingly low in humus. Nitrate is present in the *Cornus* soil to the same extent as at the other West Virginia locality studied.

The measurements of soil temperature here reported were made so near to the time of year when weather records indicate the maximum to be attained that they are believed to approximate the highest temperature to which the roots of *Cornus canadensis* are subjected at the localities concerned.[3] It seems safe to conclude at any rate that this never exceeds 65° F. or 18° C. This low temperature evidently slows up the decomposition of the vegetable debris present, and favors the development of a high degree of acidity—up to active acidity 315 (pH 4.5). Neither the low temperature nor the high acidity is able, however, to suppress nitrification, as the content of nitrogen in nitrate form ranged from 0.0002 to 0.0004 per cent (2 to 4 parts per million). Soils with similar acidity values and nitrate contents are frequent in many localities near the more southern stations herein studied, yet the *Cornus* seems unable to colonize them. The evidence thus favors the view that *Cornus canadensis* is a thobic (thermophobic) plant, and suggests that its migration southward is restricted by its inability to establish itself in soils which are heated above 65° during the summer.

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[3] Professor Petry advises me that in the New York glacial depressions the soil temperature tends to increase after the maximum air temperature of the season has been passed, but it seems unlikely that the increase can amount to more than a few degrees.

REVIEWS

Collembola of Iowa [1]

This is a taxonomic study with full keys for the identification of species. As the publishers say, "because these insects are largely soil and humus inhabitants, anyone interested in the ecology of soil animals will find this book a valuable addition to his library."

Frank E. Lutz

The American Museum of Natural History

Entomological Apparatus [2]

This lithoprinted book by Peterson contains numerous diagrams of entomological apparatus including much of interest in ecological investigations. The author makes no pretentions to the completeness of the material, but over a thousand figures, most of them illustrating separate pieces of apparatus, will give an idea of the extent of the work. Cages, traps, museum equipment, collecting equipment, behavior apparatus, weather recording instruments, humidity and temperature devices, water baths, etc., are all figured. Handy tables of measurements and conversion are included. This book should be in the library of every institution interested in entomological research and will find its way into the private libraries of many investigators.

A. E. Emerson

University of Chicago

The Ecology of Insects [3]

This new edition of Folsom's well known work has been revised and brought up to date by R. A. Wardle. The chapter headings of the 3d edition remain, but much additional material is evident and the sources are contained in the bibliography arranged by subject headings. The chapters of particular interest to ecologists are: Adaptations of Aquatic Insects, Color and Coloration, Adaptive Coloration, Insects in Relation to Plants, Insects in Relation to Other Animals, Insects and Disease, Interrelations of Insects, Insect Be-

[1] **Mills, Harlow B.** 1934. A Monograph of the Collembola of Iowa. xi + 143. Collegiate Press, Ames, Iowa. $2.25.

[2] **Peterson, Alvah.** 1934. A Manual of Entomological Equipment and Methods. 21 + xiii pp., 138 pls., 12 tables. *Edwards Brothers, Ann Arbor, Michigan.* $3.75.

[3] **Folsom, J. W., and R. A. Wardle.** 1934. Entomology with special reference to its ecological aspects. 4th ed. viii + 605 pp., 5 pls., 308 figs. *P. Blakiston's Son & Co., Philadelphia.* $4.00.

havior, Distribution, Insect Ecology, and Insects in Relation to Man. The book does not exhibit the bias toward the purely experimental and quantitative aspects of insect ecology evident in such works as Chapman's textbook of "Animal Ecology" and thus presents important material not contained in other general works. However, Chapman's book presents a more rigidly critical viewpoint in the fields of insect ecology with which it deals.

Folsom and Wardle's book is readable and is presented in an interesting manner. It is eminently suited as a textbook for undergraduate work in this field and will doubtless be an important reference work for all general courses in ecology.

A. E. Emerson

University of Chicago

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NOTES AND COMMENT

Note on the Lime Values Given in the Paper "Types of Humus Layer in the Forests of Northeastern United States," by L. G. Romell and S. O. Heiberg, Ecology 12: 567–608, 1931

The data referred to in the title are not reliable, as shown by later determinations on "available" lime. These mostly gave figures higher than the earlier values of total lime, for the same samples. Control analyses on half a dozen samples where the disagreement was worst proved the old values to be very seriously too low. From a comparison with all the new data on "available" lime, the old total lime figures appear as mostly too low and relatively much more so with low lime contents. The source of the errors in the old analyses is probably that at that time iron and alumina was mostly precipitated only once, following the directions p. 105 in the well-known Manual "Standard methods of chemical analysis" by Scott and others, vol. 1, 3d ed., New York, 1922. This may give very seriously too low results with little lime and much sesquioxides present, as is frequently the case in forest soil samples. Even with double precipitation of iron and alumina, the values may come out too low. This is shown in a forthcoming paper by O. G. Cavetz where a citric acid method (see p. 106 in the Manual just quoted) is advocated as preferable to the more common methods.

Fortunately, the few conclusions drawn from the lime data, in the paper of 1931, are not affected by the errors discovered. Data on "available" lime for a number of the same samples are given in a paper by C. C. Heimburger, "Forest type studies in the Adirondack region," to be published as a Cornell Memoir.

L. G. Romell

Cornell University

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I. A. R.

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